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FORAGING STRATEGIES, PATCH USE, AND CONSTRAINTS ON GROUP SIZE IN THREE SPECIES OF COSTA RICAN PRIMATES

by

COLIN A. CHAPMAN

(C)

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF DOCTOR OF PHILOSOPHY

DEPARTMENTS OF ANTHROPOLOGY & ZOOLOGY

EDMONTON, ALBERTA

SPRING 1987

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled FORAGING STRATEGIES, PATCH USE, AND CONSTRAINTS ON GROUP SIZE IN THREE SPECIES OF COSTA RICAN PRIMATES submitted by COLIN A. CHAPMAN in partial fulfilment of the requirements for the degree of DOCTOR OF PHILOSOPHY.

L. M. Fedigan

Co-supervisor

Jan O Murie

Co-supervisor

Hans Bocito

T R Mitgmore

External Examiner

Date Feb 10 1986

ABSTRACT

A quantitative description of foraging patterns, range use, and patch exploitation is provided for three species of neotropical primates living sympatrically in a tropical dry forest. This description provides a basis both for examining the importance of interspecific dietary overlap in the evolution and maintainance of dietary strategies and identifying ecological constraints on the size of animal groups. The study was conducted in Santa Rosa National Park, Costa Rica in an area of primarily dry deciduous forest. Over a 4-year period (1982-1986), 24 months were spent in the field studying one group of each of the three primate species in the park: spider monkeys (Ateles geoffroyi), howling monkeys (Alouatta palliata) and cebus monkeys (Cebus capucinus). The behaviour, diet, and range use patterns of each of the three primate species were simultaneously quantified in 3-week sampling periods. At the end of each period, the phenological status, size, density, and distribution of each of the primate species' food resources were determined in three 4-hectare grids.

Although the climate of the region is highly seasonal, and previous studies have suggested that such seasonality corresponds to the changes in food availability, data presented here indicate that both season and food availability are poor predictors of diet and range use patterns. The food resources used by the primate species normally occurred in patches. Spider monkeys generally depleted the food trees (patches) they used and howling monkeys depleted the fruit patches they used, but not those patches in which they ate leaves. That suggests that one primate species could limit the availability of shared food resources to a second monkey species. However, the temporal variability of dietary strategies and dietary overlap of these three primate species indicates that dietary overlap may only act as a selective pressure determining diet choice on an intermittent basis.

Analyses of the size of the subgroups formed by the spider and howling monkeys and the corresponding ecological conditions experienced by the animals, suggest that group size can be constrained by ecological conditions. It was possible to predict the relative size of subgroups based on the size, density, and distribution of food resources, such that when food patches were small, rare, and clumped, small subgroups occurred, whereas when patches were

large, abundant, and uniformly distributed, spider and howling monkeys were found in large subgroups. In contrast, cebus monkeys did not respond to changes in these ecological variables by either forming subgroups or by altering the spatial cohesion of their group. The difference between the species may be related to the differential risk of predation, with cebus monkeys, the smallest of the three species, experiencing greater predation pressure than the spider or howling monkeys.

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I. Introduction

Recently, there have been several attempts to formulate principles that govern the size of animal groups and to predict how animals are distributed in space (see reviews by Altmann 1974, Clutton-Brock 1977, Pulliam and Caraco 1984). Most notably, food resources have been suggested to influence how animals are associated. A primary goal in the field of behavioural ecology is to develop theories to explain the foraging strategies and social organization of animals by identifying selective pressures that underlie such traits. These theories assume that behaviours associated with predictable ecological patterns are adaptive in their present environment and that their existence can be explained by natural selection. Although testing this assumption directly is difficult (Gould and Lewontin 1979), such an approach seems promising for understanding variation in animal group size, foraging strategies, and social organization.

The density and distribution of food resources have been invoked as primary determinants of foraging strategies (Altmann 1974, Bradbury and Vehrencamp 1976a,b, Clutton-Brock 1974, Horn 1968, Terborgh 1983) and association patterns (Jarman 1974, Klein and Klein 1975, 1977, Leighton 1982, Ward and Zahavi 1973), and have been said to influence whether or not animals defend exclusive areas (Brown 1964, Schoener 1971). Many approaches have been used to examine how resource density and distribution might influence animal spacing and group sizes, including the comparative approach (Clutton-Brock and Harvey 1977, Crook 1965, 1972), outlining basic rules of foraging and grouping (Altmann 1974), experimental approaches (Caraco et al. 1980, Krebs 1980), and the development of simple models (Bradbury and Vehrencamp 1976b, Horn 1968).

Despite the relative importance placed on food resources as selective agents of foraging strategies and group size, the development of this area of investigation has been limited by a number of problems. For example, variation in the foraging strategies, group size, and the patterning of food resources of a single population has rarely been documented. Thus, descriptive data necessary to understand the responses of animals to different environmental conditions are scarce. Subsequently, the most frequently used method of

investigating the influence of resources on group size is interspecific comparisons. This method is limited by our inability to separate differences due to phylogenetic inertia or sampling techniques from those associated with variable responses to differing conditions.

A second problem, which is particularly relevant when using the comparative approach, is the tendency to view diets in terms of inflexible categories (e.g. frugivore or insectivore, Richard 1985). The boundaries between such categories are not always rigid and clear cut; rather, individuals, groups, and species may be flexible with respect to diet.

A third problem is that the resource variables considered important in determining foraging strategies and group size are rarely defined in terms relevant to the study animals and are rarely measured quantitatively. Commonly, resources are viewed as qualitative dichotomies (e.g. Clutton-Brock 1975, Emlen and Oring 1977, Horn 1968, Klein 1972). Such studies simply define resources as being clumped (patchy) or uniform (even) with respect to spatial pattern, predictable or unpredictable in temporal distribution, and as being dense (abundant) or sparse (rare). Given the theoretical significance attributed to these variables, dichotomous classification is inadequate. Such factors should be defined as continuous variables and the patterning of resources that constitutes a "patch" should be described in terms appropriate for the study species. Resource patches will likely be difficult to define because food resources may be aggregated on a number of spatial scales (Pielou 1969), and an appropriate scale must be defined for each situation and species. The selection of an appropriate spatial and temporal scale for a given species and situation will depend on the study subject's movement capabilities, foraging strategies (including energy and nutrient needs), digestive efficiency, and on the spatial and temporal patterning of the resources in their environment.

Finally, to understand how different foraging strategies might affect an animal's fitness and the probability that specific traits, such as a group size, are maintained by selection, it is necessary to examine the extent of variability in foraging strategies. Foraging strategies have typically been considered as consistent for all populations of a species (Richard 1985). However, under certain circumstances foraging strategies may prove flexible, thus altering the processes potentially capable of explaining their evolution (see Rotenberry 1980,

Wiens 1977, Wiens and Rotenberry 1979).

The objective of this study was to examine the foraging strategies of the three species of primates (Ateles geoffroyi, Alouatta palliata, Cebus capucinus) found in Santa Rosa National Park, Costa Rica and to investigate how inter- and intraspecific variation in the exploitation of resources can influence their group size. In the second chapter I describe the foraging strategies of the three primate species and document how seasonal variability of resources affects the study groups' behaviour and ranging patterns. In Chapter 3 I address the question of whether or not these primates use resources that can be considered to occur in patches, and subsequently examine the important assumption that patches are depleted as a result of primate foraging pressure. Chapter 4 examines the variability that was observed in the diets of these three species in the 4 years of study in an attempt to assess the probability of diets evolving in response to commonly suggested ecological pressures, such as interspecific dietary overlap. I also examine how well classical categorization of primate diets represents the actual feeding behaviour of the monkeys. In the last chapter I draw upon analyses in the previous chapters to examine whether or not the density and distribution of food resources sets limits on the size of the primate groups. This study does not attempt to directly examine the selective agents behind the evolution of group living. Rather, I assume such selective pressures exist and examine the influence of ecological factors that limit group size, in particular the size, density, and distribution of resources.

The primates of Santa Rosa National Park offer an excellent opportunity to investigate primate foraging strategies and certain ecological influences on group size. Not only do these three species differ in social organization, but also the pattern of association varies over time. This natural variation is valuable, as an attempt can be made to relate variability in association patterns to predictable environmental conditions and to examine general models of group size. Secondly, although these three primate species are often categorized as having very different diets, a major food resource of all three species is fruit. Fruit occurs in relatively discrete locations and can easily be classified as available or unavailable, since most fruiting species change their outward morphology in association with

ripening (Janson 1983). That allows the resource variables that could influence animal group size to be clearly defined. Finally, the behaviour of the primates of Santa Rosa National Park is easy to observe and quantify, facilitating the assessment of relationships between behaviour and ecological conditions.

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II. Patterns of Foraging and Range Use by Three Species of Neotropical Primates

Introduction

A growing number of field studies have documented marked variation in the diet and range use patterns of primates. This variation is frequently suggested to be a response to varying environmental parameters, such as the abundance, distribution, or quality of food resources (Clutton-Brock 1974, Harrison 1983, Klein and Klein 1975, 1977, McKey and Waterman 1982, Raemaekers 1980, Wrangham 1981). Variation in diet and movement patterns have also been attributed to the availability of safe resting sites (Altmann and Altmann 1970, Hamilton 1982, Kummer 1968, Rasmussen 1979), the digestive capabilities of the study species (Milton 1980), body size (Clutton-Brock and Harvey 1977, Milton and May 1976, Terborgh 1983), disease control (Freeland 1976), and factors such as the availability of mates and the presence or absence of competitors and/or predators (Rasmussen 1979, Mitani and Rodman 1979).

To understand interspecific variation in behavioural responses to dynamic environmental conditions, it is useful to study species inhabiting the same habitat, thereby eliminating variability between sites in potentially important, but unmeasured, variables. In addition, it is valuable to study synchronously all of the species for which comparisons will be made, since the density and distribution of shared food resources can change rapidly as a result of phenological changes in their food plant species. Different primate species are often studied at the same location (e.g. Struhsaker 1978, Terborgh 1983), but rarely are all species studied synchronously (but see Gautier-Hion 1980, Gautier-Hion et al. 1980, MacKinnon and MacKinnon 1978, 1980).

The objective of this investigation was to describe the diet and range use patterns of the three species of primates found in Santa Rosa National Park, Costa Rica, (Ateles geoffroyi, Alouatta palliata, Cebus capucinus) and to examine the variation in these variables as they relate to seasonal changes and concomitant changes in food availability. Santa Rosa

offers an excellent opportunity to determine if diet and range use patterns change in relation to season, since the climate of the region is highly seasonal. From mid December until the end of May little if any rain falls in the park, and most of the non-riparian trees lose their leaves. Such environmental variation is likely to create situations where food availability differs markedly between seasons, as plants often synchronize fruiting, leaf flush, and flowering events to coincide with the rains.

Methods

The study was conducted at Santa Rosa National Park, Costa Rica during a total of 24 months in the field (July and August 1983, January to August 1984, January to July 1985, February to August 1986). During the final field season, only spider monkeys were studied. Santa Rosa is situated 35 km northwest of Liberia, Guanacaste, adjacent to the Pan-American highway. Rectangular in shape and covering approximately 10,800 ha, Santa Rosa consists of a series of stepped plateaus which start at an elevation of 300 m and drop to the ocean. The area was originally a dry deciduous forest dominated by clumps of oak forest (Quercus oleoides). Over the past 300 years, however, much of the upper plateau was cleared for cattle pastures. With the establishment of the park in 1971 and the removal of the cattle in 1978, some of the grassland areas have gradually reverted to woody vegetation, while others have been maintained by repeated burnings. The vegetation of the park is consequently a mosaic of grassland (Hyparrheia rufa), dry deciduous forest containing Spondias mombin, Luehea candida, L. speciosa, Guazuma ulmifolia, Bursera simaruba, and Chlorophora tinctoria, and semi-evergreen forest containing Hymenaea courbaril, Mastichodendron capiri, and Manilkara chicle (Bonoff and Janzen 1980, Janzen 1982a,b,c, 1986, Chapman unpublished data). To facilitate access to remote areas, a system of approximately 20 km of trails was established in the area over the duration of the study.

The climate of the region is characterized by two distinct seasons; the dry season extends from approximately mid December to late May, and the wet season encompasses the remainder of the year. Rainfall in Santa Rosa ranges between 900 and 2400 mm annually,

almost all of which falls in the wet season (Appendix 1:2A). During the dry season the majority of the non-riparian trees lose their leaves and remain bare until the rains.

Single groups of each of the three primate species, whose home ranges overlapped extensively, were chosen as study subjects. The howling monkey group had on average 40 individuals; 7-8 adult males, 16-18 adult females, 1-2 large immature males, 1 large immature female, 4-6 small immatures, and 6-9 infants (see Fedigan et al. 1985 for a description of the age/sex classes used). Howling monkeys have typically been described as living in relatively stable, cohesive, multimale-multifemale social groups (Chivers 1969, Estrada 1984, Gaulin et al. 1980, Gaulin and Gaulin 1982, Glander 1980, Milton 1980, Smith 1977). The study group had a multimale-multifemale type of social structure, but was neither stable nor cohesive. The group frequently divided into subgroups which were spatially separated for periods that lasted up to 4 weeks.

The cebus monkey group contained on average 26 individuals; 2-4 adult males, 9-10 adult females, 4-5 large immatures, 5-6 small immatures, and 0-4 infants. This was a large group for Santa Rosa; the mean cebus group size for the park was 14.0 individuals (Fedigan et al. 1985).

An exact count of the size of the spider monkey study group was not possible because of the fission-fussion type of social organization possessed by spider monkeys (Fedigan and Baxter 1984). However, the minimum size of the community was obtained by summing the maximum counts of all age/sex classes seen in 1 year. Using this method the community was estimated to contain 42 individuals; 4 adult males, 17 adult females, 2 large immature males, 4 large immature females, 7 small immatures, and 8 infants (see Chapman and Fedigan unpublished data).

Behavioural Observations

Behavioural data were collected using a focal animal sampling regime to obtain the most complete record of not only what the subject did, but also of what was done to the subject (Altmann 1974). With this sampling procedure, 394 hours of focal animal data were collected on howling monkeys, 335 hours on the spider monkeys, and 171 hours on the cebus

monkeys, for a total of 900 hours. Normally the species chosen to be sampled was alternated each day, although this depended somewhat on the ease with which each species could be located on a particular day. The length of the focal animal session was set at 10 minutes, and if the subject was lost prior to the end of the session, the session was terminated and the data discarded. When possible, the animal to be sampled was chosen according to a fixed rotation between age/sex classes (the identity of the individual was not always known). An attempt was made to obtain a complete record of each species' activity during a 3-week sample period so that at the end of this period approximately an equal number of observations were made in each hour of the day.

Location of the group being followed was recorded every 10 minutes as a coordinate on a 120 m by 120 m grid superimposed on an aerial photograph of the study area. Since known individual trees could often be identified on the photograph, I felt that error in estimating location was small, and rarely resulted in the group being recorded in the wrong cell of the grid. Home ranges of the cebus and howling monkey groups were considered to be the sum of those cells of the grid that group members were seen using, or would have had to pass through to get from the location of one sighting to that of another sighting made on a subsequent day.

Ecological Sampling

To quantify the size, density, and distribution of food resources, the most commonly used food plant species (see below) were identified for each primate species from the preceding 3 weeks of behavioural observation, and the location, size, and phenological status of all adult trees of these species were determined in three 4-hectare grids. An adult tree was considered as any individual that had attained a diameter at breast height (DBH) greater than or equal to that of the smallest individual known to bear fruit. The three grids were 200 m by 200 m and each grid consisted of 400 cells that were 10 m by 10 m in size. Corners of the cells were marked with an individually labeled steel post. The three grids encompassed 9.0% of both the cebus and howling monkeys home ranges. Each grid was established in a different type of habitat, such that all major habitat types used by the monkeys were sampled (Appendix

1:1B). The phenological information recorded involved assessing the stage of leaf development (no leaves, leaf buds, young leaves, mature leaves) and noting the presence or absence of fruit and flowers. In 1984, phenological data were recorded on the plant species which the preceding 3 weeks of behavioural sampling had demonstrated to be important. In 1985 and 1986 the phenological status of all individuals of the major plant species used by the primates any time during the study were determined. After January 1985 when a plant species was used which had not been eaten in the past, phenological data were recorded on it in all subsequent ecological sampling periods. Normally only four plant species were chosen to represent the ecological conditions for a 3-week period. The use of only four major plant species in each period seems appropriate since they always accounted for over 91% of all of the time spent feeding. The 3-week sampling period was chosen because within that time an adequate sample of each species behaviour could be obtained and because the phenological cycles of the majority of the food plants used by the monkeys changed little over that period. Individuals of the few species of plants that were exceptions to this (eg. flowering Tabebuia ochracea) could be identified by looking for food items that had fallen to the ground. Thus, food resources were not so ephemeral that they could not be sampled accurately or that the primates could not respond to the changes.

To determine the distribution of the adult trees that were bearing food items, the "Coefficient of Dispersion" (CD) was calculated (Milton 1980, Pielou 1969, Sokal and Rohlf 1981, Southwood 1966). The value of the CD is greater than one when the distribution pattern is clumped, less than one if the pattern is uniform, and equal to one if the pattern is random. The density of food trees was simply the number of food trees in the grids, divided by the area of the grids. The selectivity of a particular food item was measured as the proportion of the total time spent feeding on that food item, divided by the density of the adult trees that supplied that food item. Thus, high values indicated selection for an item.

Food Abundance

The abundance of the food resources available to each of the three primate species was calculated separately for each sample period. Abundance would ideally be represented as

the number of food items in all the patches available; however, because the large number of trees used by the monkeys precluded counting food items, the abundance within a tree was represented as diameter of the tree measured at breast height (DBH). For several tropical tree species, DBH has been shown to be a reasonably accurate reflection of the reproductive capacity of fruiting individuals (Leighton 1982, Leighton and Leighton 1982, McDiarmid et al. 1977, Peters et al. in prep.). To calculate a relative measure of food abundance for comparison between time periods, the size all of the food trees found in the gridded areas that were bearing food items was summed and this value was divided by the area of the grids.

By studying each of the three primate species simultaneously, it was hoped that more confidence could be placed in discussions of the significance of correlations. If strong similarities existed between the species in correlations of the same variables, then it is less likely that the results occurred by chance than would be the case if the relationships were found for only one primate species.

Results

Foraging Strategies

Over the duration of the study the cebus and spider monkeys spent the greatest proportion of their feeding time eating fruit; 81.2% and 77.7% respectively (Table 1). In contrast, the howling monkeys were more folivorous; they spent 49.0% of their feeding time eating leaves, and only 28.5% of their feeding time eating fruit. The cebus were the most insectivorous of the three species. They spent 16.9% of their feeding time eating insects. Unlike both of the other species, cebus monkeys virtually ignored both leaves and flowers. On a monthly scale, the types of food eaten varied considerably (Chapter 4). For instance, the diet of the cebus monkeys varied between sample periods from being entirely insectivorous (100% of their feeding time), to being primarily frugivorous (97.1% of their feeding time).

All three species fed on parts of a variety of plant species. Appendix 1 depicts the percentage of each group's feeding time spent eating food items which constituted more than 1% of their respective feeding efforts over the entire study. The use of foods that constituted

less than 1% of the observed feeding time represented feeding bouts of such short duration that the probability of observing them were largely a matter of chance. Using the 1% criterion, the howling monkeys had the most varied diet; they were observed eating 22 different food items from 11 species of trees. The spider monkeys ate 20 different types of food items, from 18 plant species and the cebus monkeys ate 14 different plant food items from 13 different species. Even though all three species ate many different types of food items, a few of them constituted the bulk of each species' feeding efforts. The cebus monkeys spent over 50% of their feeding time during the study eating only two different types of food items (Sloanea terniflora fruit, Muntingia calabura fruit). Spider monkeys spent more than 50% of their feeding efforts eating only three foods (Muntingia calabura fruit, Ficus sp. fruit, Mastichodendron capiri fruit), while howling monkeys spent over 50% of their feeding time eating 6 different types of food items (Ficus sp. fruit, Brosimum alicastrum leaves, Manilkara chicle flowers, Pithecellobium saman flowers, Brosimum alicastrum fruit, Lonchocarpus costaricensus flowers).

All three species tended to be selective in what they chose to eat, often relying heavily on tree species that occurred at low densities (Table 2, Appendix 1:3). For instance, the heavy reliance of the spider monkey on the fruit of Mastichodendron capiri, which was the third most heavily used food item, constituting 6.6% of their feeding time, was almost exclusively the result of their feeding on two individual trees. Another similar example is the use of Swartzia cubensis fruit by all three of the primates. When this plant species was in fruit, all three primate species fed heavily on it, even when there was only 1 fruiting individual in the 12-hectare gridded area, and only three individuals in the groups' home ranges. Since some of the most used food trees occurred at low density, it was concluded that the three primate species were relatively selective in their choice of food items. For all primate species the range in selectivity between plant species was large (spiders 0.1-56.3, howlers 0.1-31.0, cebus 0.1-24.7, Appendix 1:3). The average selectivity exhibited by the three primate species were; spiders 13.5, howlers 6.0, and cebus 8.1. This selectivity index did not differ significantly between the primate species ($F=1.26$, $P=0.294$).

All three monkey species used food resources that had a clumped distribution pattern (CD = 1.25 cebus, 1.19 howlers, 1.18 spiders). No significant differences between the three species in the spatial distribution of their plant food resources ($F=0.454$, $P=0.638$). Similarly, all three primate species used plant food resources that occurred at a low density (cebus 6.46 individuals per ha, spiders 4.76 individuals per ha, howlers 7.96 individuals per ha; average density over all sample periods, Appendix 1). There were no significant differences in the densities of the primates' plant food resources ($F=1.32$, $P=0.278$).

Range Use Patterns

The size of the cebus and howling monkey home ranges were calculated as the number of 120 m by 120 m grid cells that the groups were observed using, or would have had to pass through to get from one observation point to another (Figure 1 and 2). Both groups had a 1.08 km^2 home range when observations from 1984 and 1985 were combined. Of the total area used by the cebus and howling monkey groups, 81% was used in common. The areas used by both cebus and howlers changed over the period of observation. In 1984 the howling monkey group used an area of 0.907 km^2, while in 1985 it used 0.806 km^2. In 1985 the group used 21 grid cells (36% of the total grid cells used) that they were not seen to use in 1984. The majority of the new cells entered (57%) were in areas on the periphery of the group's 1984 home range. The remainder of the new areas (43%) that were used in 1985 were cells within the 1984 home range and probably represent areas that were previously used but for which no record had been obtained. In 1984 the cebus monkey group had a home range of 0.89 km^2, while in 1985 the group used an area of 0.78 km^2. In the second year, the cebus monkey group used 18 new grid cells, 72% of which were in new areas on the periphery of their home range and 28% were cells that were within the 1984 home range, but for which no record of use had been obtained previously.

By plotting the number of new grid cells used by the either of these two primate species in each of the sample periods against time, it was evident that there was a general decline in the number of new cells that the groups were seen to enter in 1984 as the year progressed, but at the start of the 1985 season the number of new cells used increased sharply.

only to decrease as the season continued (Figure 3). This suggests that the home range of both the cebus and howling monkey groups shifted between years.

Following Kavanagh (1981), core area was defined as those 120 m by 120 m cells used by the group for more than 10% of the observations. Using this definition the core area of the howling monkey group represented 12% of the their home range and 54% of the observations. The cebus monkeys' core area similarly represented 12% of the group's home range, but observations in these areas accounted for 60% of the sightings of the group (Figures 1 and 2). The core areas for both of these species tended to be in habitats of relatively wet semi-evergreen forest and areas outside of the core areas tended to be areas of seasonally dry semi-deciduous forest (Appendix 1:1B). The cebus monkey group had 78% of their core area in the wet forest and the remainder (22%) in dry forest. For the howling monkeys, 67% of their core area was in wet forest and 33% in dry forest. This suggests that both groups were selecting areas of semi-evergreen forest in preference to dry deciduous forest. The reality of the groups treating these two habitat types differentially can be examined by quantifying each group's distribution in the different habitats. Both the cebus and howling monkeys exhibited a clumped distribution pattern over their home ranges (cebus CD=1.58, howlers CD=1.76). However, within each habitat type their distribution was uniform (howlers semi-evergreen CD=0.987, deciduous CD=0.617; cebus semi-evergreen CD=0.586, deciduous CD=0.887). For the howlers the use of the semi-evergreen forest represented 50.0% of the observations, while this forest type represented only 12% of the group's home range. This differs significantly from what would be expected if the group used the habitats in proportion to the area of each ($X^2=71.2$, $P<0.01$). For the cebus monkeys the use of semi-evergreen forest represented 57% of the observations, but this type of habitat only accounted for 14% of their home range. Again, this differed significantly from what would be expected if the group used the habitats in proportion to the area of each ($X^2=55.0$, $P<0.01$).

There was considerable variability between sample periods in how each of the species used their home range. For instance, the percentage of their home range used by the cebus monkey group per sample period ranged from 8% to 27%. The howling monkey group's use of

their home range varied from 5% to 32%. The number of grids that the groups fed in or passed through in a sample period ranged from 18 to 117 cells for cebus monkeys, and from 7 to 67 cells for the howlers.

The three species employed different foraging strategies which resulted in each species using their home range slightly differently. The howlers often stayed in close proximity to individual food trees for long periods of time (maximum 14 days). The group only left these food trees to make short excursions to feed nearby. When the group finally left such areas they tended to make long excursions to new feeding areas. This pattern of movement was reflected in the group's temporal use of their home range. On average 61% of the grids used in one sample period were used in the immediately subsequent period (range 0%-89.4%).

In contrast to the howlers, the food trees that the cebus monkeys selected rarely became focal points of the group's activity. Rather, the group tended to move from one individual tree of a preferred species to another, or they would make foraging excursions away from large individual fruiting trees only to return several hours later. This type of movement pattern resulted in a temporal pattern of home range use that differed from the howling monkeys. On average, 57% of the grids used by the cebus monkey group in one sample period were used in the subsequent period; however, unlike the howlers, this value did not vary greatly among sample periods (range 47%-88%).

Individual spider monkeys often either centered their activity around one large food tree or repeatedly fed in several spatially separated trees, often moving between feeding sites in a set pattern during the day. The spider monkeys travelled in relatively small subgroups (mean=4.54 individuals, n=704 subgroup encounters, range = 1-28) which changed composition frequently. As a result of this type of social organization, their range use patterns cannot be analysed on a group level, but rather by analysing the movement patterns of recognizable individuals (Appendix 1:4). This level of analysis is limited because the days when known individuals were followed are few in number. Nineteen spider monkeys were individually recognizable by either natural markings or from markings placed on the animals following darting and capture (see Glander et al. in prep. for a description of darting and

marking techniques). On average, an individual was seen on 37.6 occasions, and the number of sightings per individual ranged from 13 to 89. An individual's range size was considered as the number of grid cells that the animal was seen to use or would have had to pass through to get from the location of an observation made on one day, to the location of a sighting made on a subsequent day. The average range size was 43.7 hectares (range 24.5 ha to 63.4 ha) (Table 3, Appendix 1:4). These values of individual range size should only be considered as preliminary estimates, since they are based on relatively few sightings and there was a significant relationship between the number of sightings of an individual and their range size ($r=0.654$, $P=0.004$). That indicates that it is likely that as more sightings of individuals are obtained the estimate of their range size will increase.

A minimum home range for the community was calculated by summing the number of grid cells used by all of the identifiable spider monkeys, and those that they had to have passed through. Considering home range in this fashion, the spider monkey community used an area of 1.47 km^2 (Figure 4). Individuals seemed to use their range differently; some were seen frequently in a relatively restricted area (approximately 8 ha) and infrequently outside area, while other individuals were more widely dispersed across their range. This was quantified by using the Coefficient of Dispersion (CD, standard deviation of the number of sightings per cell divided by the mean). This index averaged 1.71 for all animals, and ranged from 0.6 to 5.2 (Table 3). This indicates that the location of the sightings of adult females with either infants or small immatures tended to be seen frequently in a central area and thus have a more clumped pattern of distribution (CD=2.2), whereas females without immatures were more evenly dispersed in the use of their range (CD = 1.5). This was not always true for all individuals. In one instance a female with a clinging infant had a CD lower than the average CD for females without an infant or small immature.

One identifiable adult female was accompanied by her offspring in 1984 and 1985, while in 1986 this offspring was primarily ranging independent of his mother. Between these two periods the distribution of sightings of this female became relatively less clumped (CD without a an infant = 1.8m; with an infant CD = 2.2). This observation suggests that when

a female is accompanied by an offspring she tends to concentrate her activity in a small area, only rarely making excursions away from this area. In contrast, when a female is not accompanied by an offspring, she tends to range more widely. Observations suggest that when females with accompanying offspring leave their central area, they become members of a large subgroup, often containing males.

Use of Water Resources

Santa Rosa experiences a long, severe, dry season, during which most of the non-riparian trees lose their leaves (Appendix 1:2 A,B). It seems likely that during the dry season, particularly near the end of May, the availability of water influences the ranging patterns and diet of the three primate species. During the early dry season, water was available to primates from three sources: arboreal water holes, standing water that remained in creek beds, and water contained in their food resources. In the study area both the arboreal water holes and the standing water sources in creek beds dried up before the end of the dry seasons. For approximately the last 2 months of the dry season, the only water that was available to the monkeys was contained in the foods they ate. Behavioural responses to this restricted access to water were most evident in the cebus monkeys. By the end of February, when most of the non-riparian trees had lost their leaves, the cebus monkey group started to center their activity around the few remaining water holes in a creek bed in the dry forest part of their range. The group made repeated foraging excursions away from the water holes, only to return every 3-6 hours to drink. In essence they became central place foragers, centering their activity around the few remaining water holes. Once these water holes became dry, the group left the area of the creek bed almost entirely and tended to center their activity in an area of semi-evergreen forest where a large proportion of the trees kept their leaves throughout the dry season. During the 1985 field season, eight maximum-minumum thermometers were placed in semi-evergreen and dry deciduous sections of forest. The maximum daily temperature in the areas of semi-evergreen forest was on average 1.7 C cooler than the maximum daily temperature in the dry forest (Appendix 1:2C). The area of semi-evergreen forest was used extensively in the dry season by both the cebus and howling

monkey groups. That may have been a response by the monkeys to the differences in temperature between the forest types and the availability of water in the two areas. Yet, in the wet season, when water was readily available and the maximum daily temperature had decreased, both species still used the area of semi-evergreen forest frequently. By the end of the dry season the only water available to the cebus group came from the foods they ate. This may have influenced the group's choice of foods. For instance, near the end of the 1984 and 1985 dry seasons the cebus monkey group was eating primarily the fruits of Muntingia calabura, a fruit with a high water content (Fleming et al. 1985). However, with the start of the wet season, the group stopped feeding on Muntingia calabura, fruit almost entirely and switched to eating dry acorns of Quercus oleodies, even though the abundance of M. calabura increased.

Although responses to the availability of water were most evident in observations of the cebus monkeys, spiders were also seen coming to the ground to drink from standing water holes. While howlers were never seen to come to the ground to drink, they were frequently seen using arboreal water holes early in the dry season when they were available.

The Influence of Season on Diet and Range Use Patterns

Based on the extremely seasonal climate in the region of Santa Rosa, and on previously conducted studies of the phenological cycles of many tropical plant species (Baker et al. 1982, Daubenmire 1972, Frankie et al. 1974a,b, Opler et al. 1976, 1980, Smythe 1970), I expected that all three primate species would exhibit marked differences in diet and range use between seasons. However, when the diet and range use patterns exhibited by each of the primates in sample periods in the wet season were compared to those in the dry season, few differences were evident (Table 4). It seemed reasonable to speculate that the failure of these relationships to reach significance might have been because the cessation of the rains was not what influenced the animal's behaviour, but rather the monkeys responded to the phenological status of their plant food resources. The plants respond to seasonal changes in rainfall only after a lag period. Perhaps, the primates also did not exhibit seasonal changes in behaviour until they did not have access to arboreal water holes or standing water in the creek beds.

That normally occurred 2 months after the cessation of the rains. To test these ideas, the range use characteristics and diet of each of the three primate species expressed in the sample periods when standing water was available, was compared to when standing water was not available. These two periods corresponded closely to the periods when the majority of the trees that lose their leaves in the dry season have done so, and the time when the majority of trees have leaves. When comparisons were made in this manner, some differences in diet were evident (Table 5). Cebus ate flowers more when standing water was not available than when it was. Yet, flowers were not more available during these periods. In fact the total density of trees bearing flowers that were eaten by the monkeys was 16.3 individuals/ha in the wet season and 0.92 individuals/ha in the dry season. The cebus monkeys also fed more on insects during the period when standing water was available, than when it was not available. That would have been predicted based on the fact that insect availability is greater in the wet season (Buskirk and Buskirk 1976, Janzen 1973, and Wolda 1978a,b present information of the seasonal availability of insects in Costa Rica and Panama). Also, the cebus group spent more time feeding when water was not available to them, than when it was available. None of the range use variables varied significantly between the two periods for any of the three primate species.

The Influence of Food Abundance on Diet and Range Use Patterns

Table 6 presents correlations between range use variables, diet, and food abundance for each of the primate species. There were significant correlations between the dietary composition of the three primate species and the overall abundance of their plant food resources. For instance, the use of insects by the cebus monkeys was negatively related to plant food abundance, suggesting that they fed on insects during periods when other food resources were scarce. Similarly, both spider and howling monkeys tended to eat flowers when other plant food resources were not abundant. The range use variables did not relate to the abundance of food resources for any of the primate species.

Discussion

The diet and range use patterns of the three species of primates found in Santa Rosa National Park, Costa Rica exhibited few clear changes in relation to the shift in season or differing levels of food availability. A review of the literature for relationships between such variables indicates little consistency. For example, Clutton-Brock (1977) found no consistent trend across a broad range of primate species with respect to whether or not they responded to changes in food abundance by altering the distance they travelled. There are a number of theoretical and methodological reasons why we should not expect consistent, significant relationships between gross measures of range use or diet and food abundance and season.

(1) It is likely that many species can deal with a specific situation in a number of different fashions. For instance, if food availability decreased, a group could respond either by increasing travel time to locate more food trees, or they could travel less to decrease costs, so as to conserve energy. Another example, illustrated by this study, deals with the ability of primates to respond to environmental conditions by forming subgroups. In response to a change in food availability or conditions associated with season, the howlers or spider monkeys of Santa Rosa could change their behaviour, their subgroup size, or some combination of both (Chapter 5). When a mixed strategy such as that is used, the question of interest becomes; what determines the strategy to be used?

(2) Primates likely respond to subtle changes in the environment, and measures such as season and overall food abundance do not accurately reflect the situation experienced by the animals. I suggest that monkeys are more likely to respond to the phenological cycles of specific food plants than to season, as defined by the presence or absence of rain. Many plants have coevolved with the animals that disperse their seeds (Herrera 1985, Chapman in prep.). This coevolution often has resulted in single species or group of species staggering their fruiting periods to support a population of dispersers (Howe and Estabrook 1977). Such coevolution may have favoured plants which produce fruit not when it would be physiologically easiest (i.e. when water is available), but when dispersal was likely to be most successful. An example of how season may have little influence on phenology is illustrated by

the fruiting schedule of Ficus sp. and the monkey's use of fig fruit. One of the three species of primates in Santa Rosa ate fig fruit in 94% of the sample periods, reflecting the aseasonal fruiting cycle of figs (see Milton et al. 1982).

Observations made in this study suggest that range use is likely situation-dependent. A single fruiting tree can strongly influence the range use patterns of any of the primate species. This was illustrated in the example provided previously which suggested that the presence of a fruiting Ficus sp. or Swartzia cubensis tree in an area was strongly related to that area's use.

Another example of how range use can be situation-dependent is evident when comparisons between this and other studies are made. For instance, McKey and Waterman (1982) found that when food resources were scarce, their study group of black colobus (Colobus satanas) used peripheral areas of their home range. In this study no relationship existed between the use of the cebus and howling monkeys' core areas and food abundance.

(3) Defining what food resources are available for primate consumption is a difficult task. For instance, in 1986 the fruits of Bursera simaruba were used heavily by spider monkeys (22.8% of their feeding time in one monthly period), but in the preceding years that food item was almost totally ignored (0.10 % of the spider monkeys feeding time in 1984 and 1985). The availability of this food resource changed only slightly between the years (mean density in 1984 and 1985 = 20.8 individuals per hectare, mean density in 1986 = 19.7 individuals per hectare). If the observations of feeding on B. simaruba fruit had not been made in 1986, the 1984 and 1985 data would have suggested that it was not a food source. Similar examples concern the use of Quercus oleoides and Luehea speciosa (Chapman and Chapman in prep.).

(4) Many of the traditional measurements used to identify relationships examined here may be inadequate. For instance, tree species likely differ in the abundance of food they carry relative to their DBH. Home range has proven difficult to define conceptually (Burt 1943, Clutton-Brock 1975), as well as operationally. The size of a group's home range is likely more closely related to observer sampling effort than to many ecological variables. In this study, the cebus and howling monkey groups were still entering new areas at the end of the study, and

there was a positive relationship with the number of sightings of an individual spider monkey and the size of its home range.

(5) Since primates live in an environment that is unpredictable (inevitable when feeding on plant species that fruit asynchronously or species with many years between fruit crops), they must sample their environment by moving through their home range. Movement conducted when feeding on superabundant patches may reflect their need to sample the environment, or a need to patrol their territory.

(6) All three primate species studied here exhibited changes in diet, then returned to feeding on the original food resources that they ate prior to the change, even when the abundance of the foods remained constant (Chapman and Chapman in prep). This suggests that changes in diet may in some instances simply reflect attempts to obtain a varied diet (McKey and Waterman 1982).

In conclusion, the description of the diets and range use patterns of the three species of primates in Santa Rosa National Park and the examination of the expectation that diet and range use would be related to season and food availability, illustrated that these primate species were flexible in their response to the environment. Their behaviour was not stereotyped, but rather flexible to individual events, such as individual asynchronous fruiting trees, or the availability and location of standing water. Behavioural flexibility was also apparent in their diet. For all three species it was inadequate to classify their diet in terms of one simple category (e.g. frugivore), as is often done (Richard 1985). Over the entire study each of the species observed showed foraging preferences which would allow them to be classified in categories such as insectivore, frugivore, or folivore. However, often for any one sampling period their diet could be classified in a different category than the total sample period would suggest. Such behavioural flexibility would be advantageous in unpredictable environments.

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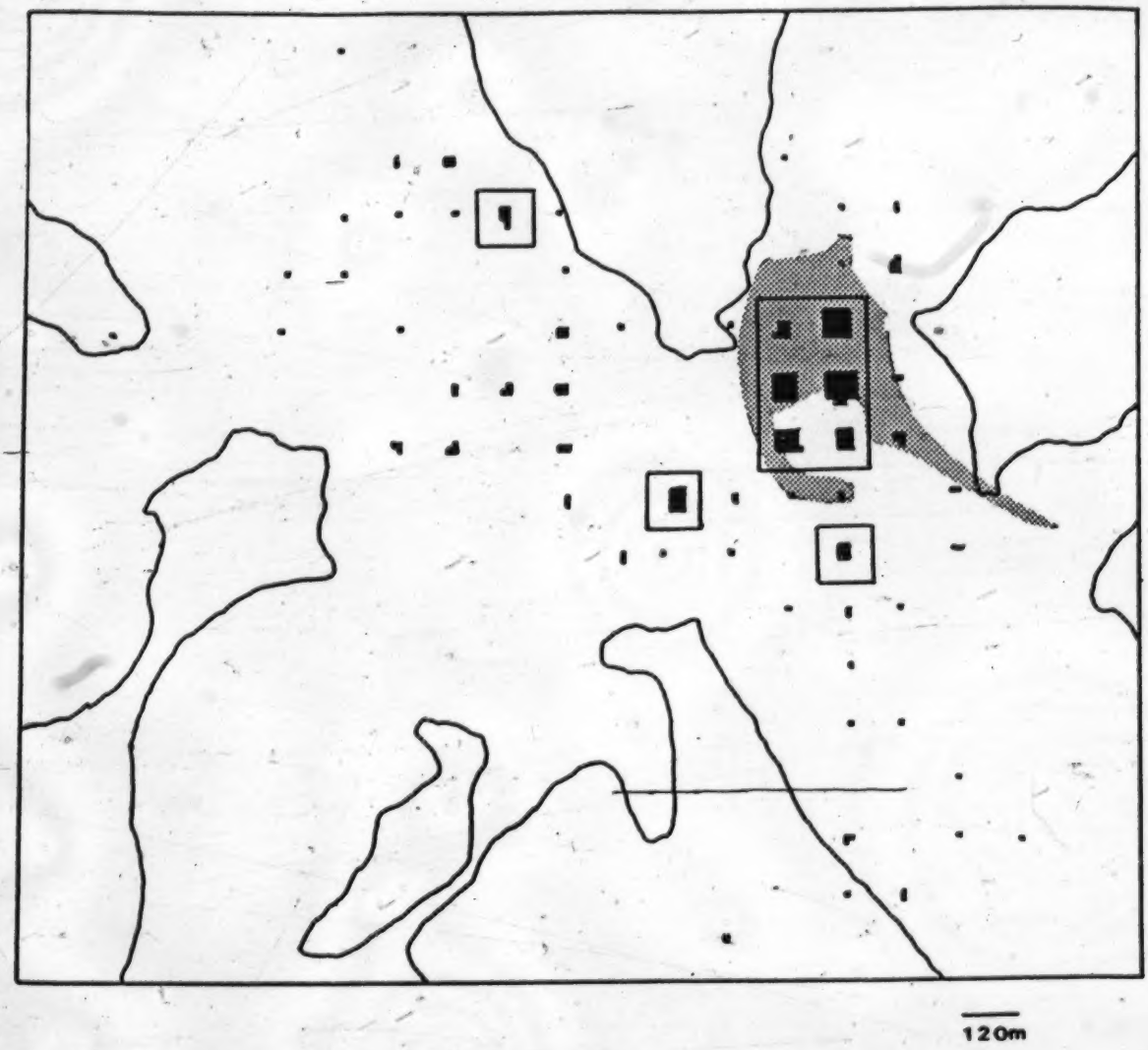

Figure 1.

The use of home range by the cebus monkey study group in Santa Rosa National Park, Costa Rica in the field seasons of the first three years of the study. The proportion of the cell that is dark represents the proportion of the total number of sightings for which the group was seen to use that area. Cells outlined in black represent the core area. Core area was defined as those 120 m by 120 m cells used by the group for more than 10% of the observations. Stippled areas represent the location of the semi-evergreen forest.

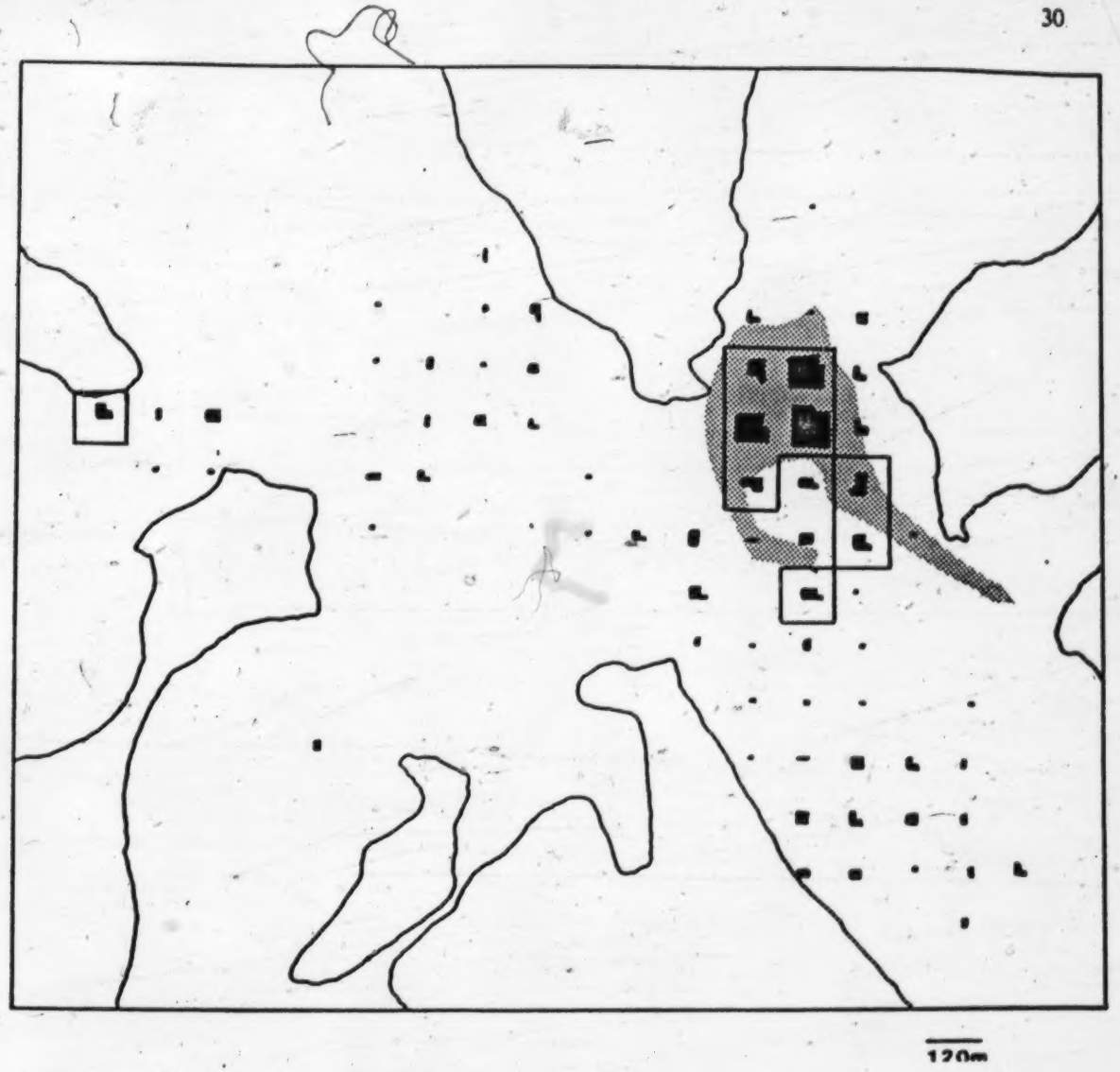

Figure 2.

The use of home range by the howling monkey study group in Santa Rosa National Park, Costa Rica in the field seasons of the first three years of the study. The proportion of the cell that is dark represents the proportion of the total number of sightings for which the group was seen to use that area. Cells outlined in black represent the core area. Core area was defined as those 120 m by 120 m cells used by the group for more than 10% of the observations. Stippled areas represent the location of the semi-evergreen forest.

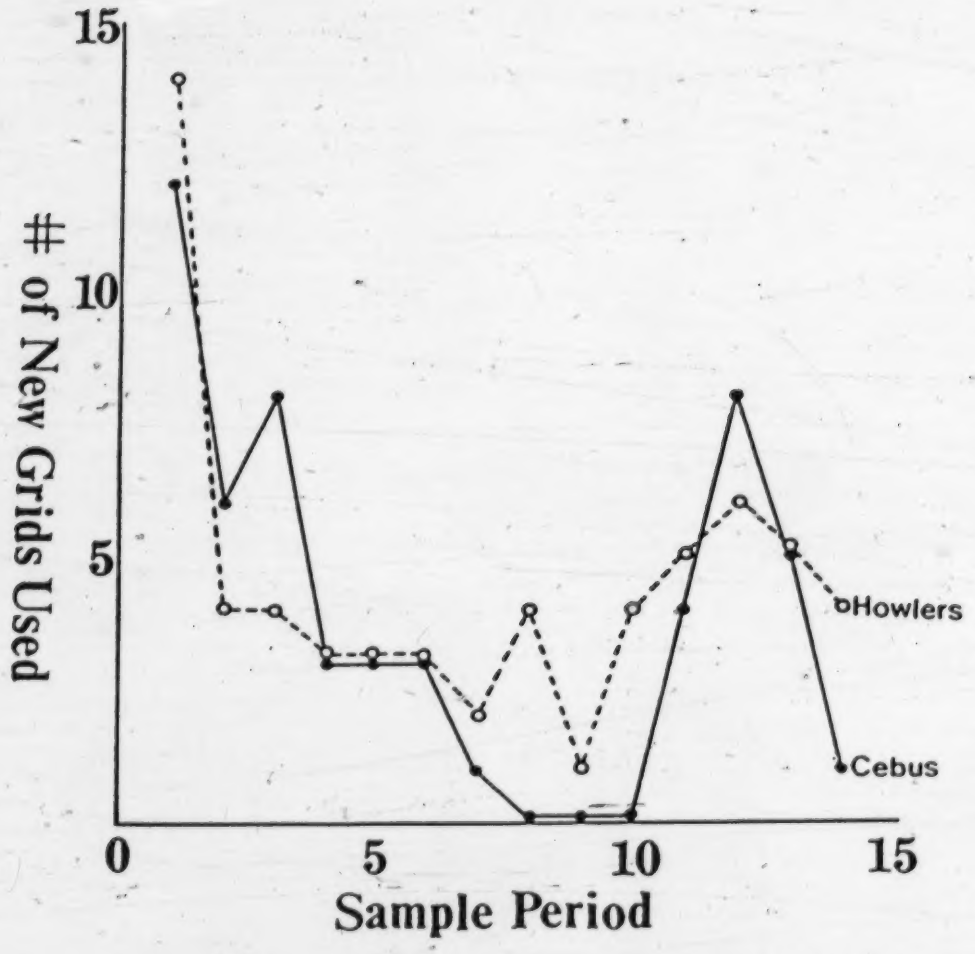

Figure 3.

The number of new grid cells that the cebus and howling monkey study groups of Santa Rosa National Park, Costa Rica were observed to enter in each of the sample periods. A grid cell is 120 m by 120 m in size (Sample periods 1 = January 15 to February 16 1984; 2 = February 17 to March 13 1984; 3 = March 14 to March 31 1984; 4 = April 1 to April 15 1984; 5 = April 16 to May 3 1984; 6 = May 4 to May 20 1984; 7 = May 21 to June 6 1984; 8 = June 8 to June 27 1984; 9 = July 1 to July 26 1984; 10 = January 25 to February 23 1985; 11 = March 1 to April 3 1985; 12 = April 7 to May 3 1985; 13 = May 10 to May 31 1985; 14 = June 4 to June 21 1985).

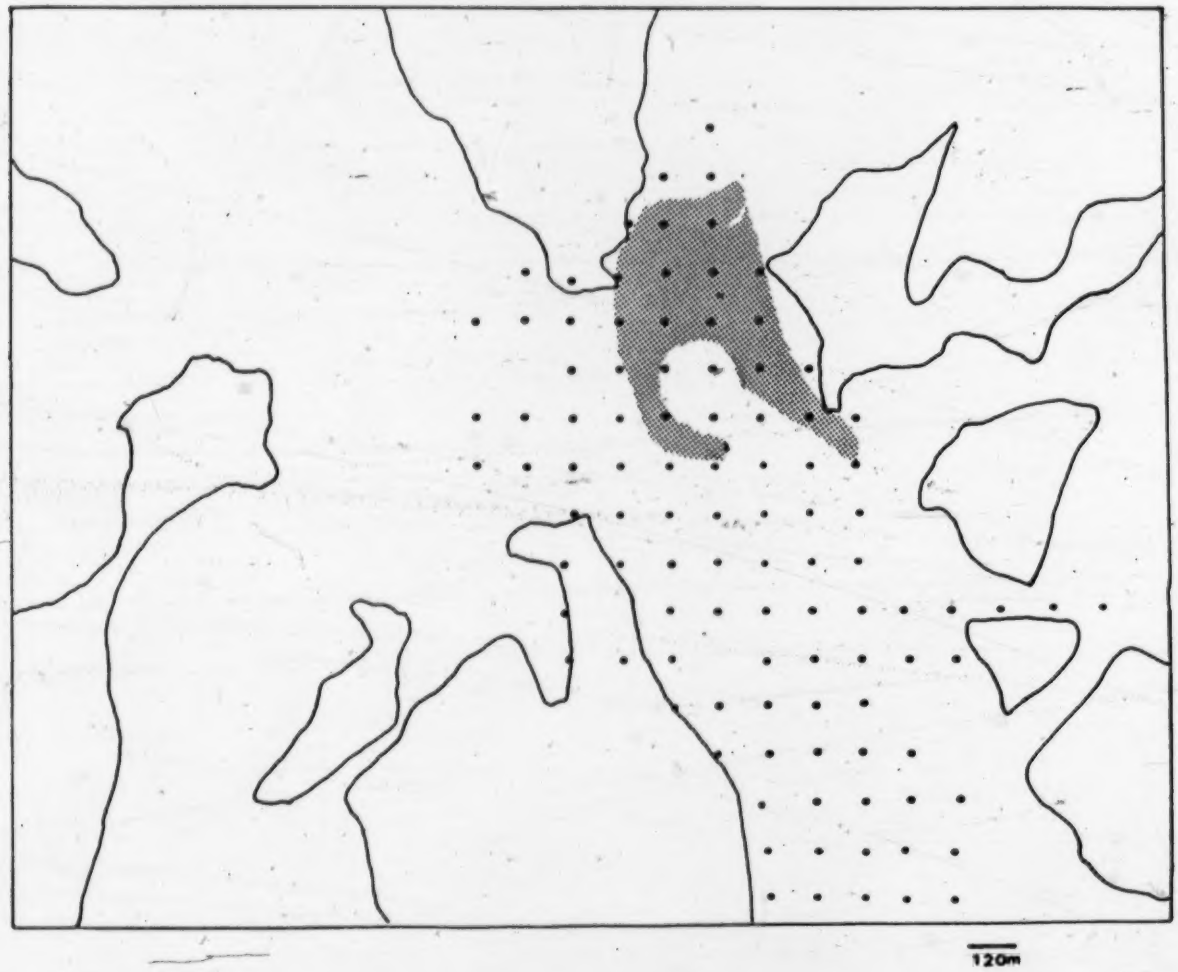

Figure 4. The use of the study area by the individually recognizable spider monkeys of Santa Rosa National Park, Costa Rica over the entire study period. The dots are at the center of a 120 m by 120 m grid cell. Stippled areas represent the location of the semi-evergreen forest.

Table 1.

Percentage of total feeding time spent eating different types of foods by the three species of primates found in Santa Rosa National Park, Costa Rica. The data are derived from focal animal observations (*Cebus capucinus* 171 hours; spiders, *Ateles geoffroyi* 335 hours; and howlers, *Alouatta palliata* 393 hours).

Plant Part		Cebus	Howler	Spider
Fruit		81.2	28.5	77.7
Flower		0.2	22.5	9.8
Leaves	Mature	0.5	27.7	1.2
	Young	0.7	17.4	7.3
	Buds	0.1	3.9	2.6
Insects		16.9	0.0	1.3

Table 2.
A description of the pattern of feeding and selectivity of the three species of primates in Santa Rosa National Park, Costa Rica, depicting the five most used plant species for each primate species.

PLANT	% of total Feeding Time	Density (ind./ha)	Selectivity
Spider			
Ficus sp. Fruit	29.2	0.6	48.5
Muntingia calabura Fruit	16.1	0.3	53.7
Mastichodendron capiri Fruit	6.6	0.3	26.4
Dipterodendron costaricensus Fruit	6.3	2.5	2.5
Pithecellobium saman Flowers	2.9	0.8	3.6
Howler			
Ficus sp. Fruit	15.5	0.6	25.8
Brosimum alicastrum Mature Leaves	10.2	0.8	12.8
Manilkara chicle Flowers	7.4	9.8	0.8
Pithecellobium saman Flowers	6.8	0.8	8.5
Brosimum alicastrum Fruit	5.5	0.8	6.9
Cebus			
Sloanea terniflora Fruit	34.1	2.3	14.8
Muntingia calabura Fruit	17.9	0.3	59.6
Luehea speciosa Fruit	4.4	19.9	0.2
Quercus oleoides Fruit	3.5	5.0	0.7
Sciadodendron excelsum Fruit	2.5	0.7	3.6

Table 3.

A description of the individual home ranges of identifiable spider monkeys (Ateles geoffroyi) in Santa Rosa National Park, Costa Rica. CD = the standard deviation of the number of sightings in the 120 m by 120 m grid callsdivided by the mean. (Dep = Dependant Infant).

Animal	Age/Sex Class	# of sightings	Home range Size in Ha	CD
1	Adult Female	14	24.5	1.2
2	Adult Female	30	53.3	1.5
3	Adult Female	13	34.6	1.2
4	Adult Female + Dep	54	37.4	5.2
5	Large Immature	26	49.0	1.9
6	Adult Male	29	51.8	0.6
7	Adult Female	38	57.6	2.0
8	Adult Female + Dep	34	36.0	1.2
9	Small Immature	32	38.9	2.4
10	Large Immature Dep	30	31.7	0.9
11	Adult Female + Dep	33	41.8	1.5
12	Adult Female + Dep	30	31.7	0.9
13	Adult Female	27	43.2	1.8
	With Dependent #14	62	44.6	2.2
	Total	89	63.4	2.3
14	Large Immature	12	36.0	2.8
	When Dependent on 13	62	44.6	2.2
	Total	74	60.5	2.1
*Average		37.6	43.7	1.71

*only totals for numbers 13 and 14 included

Table 4.

Seasonal differences in the diet and range use of the three species of primates living in Santa Rosa National Park. Presented are the mean values for dry season and wet season. (*** - <<0.01)

	Cebus		Howlers		Spiders	
	Wet	Dry	Wet	Dry	Wet	Dry
% Of Time Feeding	25.3	28.9	17.6	13.8	29.4	26.7
% Of Time Traveling	47.8	25.3***	8.4	6.7	25.6	18.7
Density of food trees	5.4	6.9	8.5	7.8	4.8	4.7
Distribution of food trees	1.4	1.2	1.2	1.2	1.2	1.2
% Fruit	67.1	79.7	26.9	26.4	75.1	70.3
% Leaves	4.2	2.2	55.3	46.9	12.1	17.0
% Flowers	0.0	0.8	21.0	26.7	7.4	10.8
Food Abundance	104.0	74.4	566.6	245.5	109.9	87.6
# Grids Used	9.8	10.8	11.3	10.1	----	----
% of Home Range	4.0	7.0	15.3	13.5	----	----
% of Time in Core Area	60.1	52.0	61.5	46.4	----	----
Distribution in Range Use	0.6	0.6	0.9	0.8	----	----
% Insects	30.3	18.4	----	----	----	----

Table 5.

Seasonal differences in the diet and range use of the three species of primates living in Santa Rosa National Park. Presented are the mean values when water is available and when water is not available. (* - <0.1; ** - <0.05; *** - <0.01)

	Cebus		Howlers		Spiders	
	Water	No water	Water	No water	Water	No water
% Of Time Feeding	38.4	22.0***	14.2	16.2	24.6	31.7
% Of Time Traveling	35.9	24.0	8.0	5.7	22.6	12.5*
Density of food trees	6.9	5.7	7.0	9.7	5.2	6.2
Distribution of food trees	1.2	1.2	1.4	1.2	1.2	1.2
% Fruit	71.1	85.1	24.3	30.6	71.4	73.5
% Leaves	1.9	4.3	51.6	45.1	18.7	6.8
% Flowers	0.1	1.5***	25.5	24.9	6.6	17.0
Food Abundance	59.7	104.0	290.2	339.0	131.4	52.0
# of Grids Used	9.7	12.0	10.4	10.4	----	----
% of Home range	12.9	16.0	14.0	13.9	----	----
% of Time in Core Area	48.8	64.9	57.1	39.1	----	----
Distribution in Range Use	0.5	0.6	1.0	0.6	----	----
% Insects	28.1	10.4**	----	----	----	----

Table 6.
The relationship between food abundance and diet and range use variables for the three species of primates in Santa Rosa National Park, Costa Rica (Pearson r values reported).

	Cebus Food Abundance	Howlers Food Abundance	Spiders Food Abundance
Feeding Time	0.64	0.66	-0.62
Travel Time	0.41	0.15	0.51
% Fruit in Diet	0.61	0.27	0.54
% Leaves in Diet	0.36	0.19	0.96**
%Flowers in Diet	0.38	-0.18	0.41
# of Grids Used	0.32	0.22	
% Home Range Used	0.37	0.23	
Use of Core Area	0.04	-0.28	
% Insects in Diet	-0.92**		

III. Patch Use and Patch Depletion By The Spider and Howling Monkeys Of Santa Rosa National Park, Costa Rica

Introduction

Many of the models proposed to explain aspects of foraging behaviour, group size, or social structure assume animals use resources that occur in patches, and that through such use the patches become depleted. For instance, a number of models developed to predict group size suggest that the costs and benefits of using patches vary with group size, such that for a given resource state there is an optimal group size which tends to maximize foraging efficiency (S. Altmann 1974, Bradbury and Vehrencamp 1976a,b 1977, Caraco and Wolf 1975, Horn 1968, Klein and Klein 1975, 1977, Leighton 1982, Leighton and Leighton 1982, Stacey 1986, Terborgh 1983, Van Schaik et al. 1983, Ward and Zahavi 1973). In opposition to the assumption of patch depletion, is the suggestion that the food resources used by primates are superabundant (Carpenter 1965, Coelho et al. 1976, Struhsaker 1978). If resources are superabundant, the assumption of patch depletion would likely be invalid. Thus, the application to primate species of models of foraging behaviour and group size, which rely on that assumption, are unlikely to accurately represent the animal's behaviour. In addition, primates may deplete only certain types of patches, or deplete patches only in specific circumstances. For instance, patches may not be depleted if food toxins, digestibility, nutrient requirements, or the actions of competitors cause a group to leave a tree prior to its depletion. Since patches may not be depleted because of reasons such as these, it is essential to determine if primates deplete the food patches they use, prior to applying any of the foraging models that incorporate this assumption to primates.

The objective of this investigation was to examine under what circumstances the spider (Ateles geoffroyi) and howling monkeys (Alouatta palliata) of Santa Rosa National Park, Costa Rica likely deplete the patches they use. Defining what constitutes a patch has proven difficult in field situations. This is partially because food resources may be aggregated

on a number of spatial and temporal scales (Pielou 1969). Thus, an appropriate scale must be defined for each situation and species. Temporal predictability is represented as the persistence of food resources at a given location once the food resource is available (Colwell 1974, Warner 1980); however, it is difficult to determine when resources are available and if an animal has sampled its environment sufficiently to know the location of the resource. The selection of an appropriate spatial and temporal scale for a given species and situation will depend on many factors including the animal's movement capabilities, foraging strategies (including energetic and nutrient needs), digestive efficiencies, and the spatial and temporal patterning of resources in its environment. A number of theoretical or conceptual definitions of patches have been proposed (Addicott et al. in prep., S. Altmann 1974, Hassell and Southwood 1978). For the purpose of this study a patch was considered as an aggregation of food items structured such that animals could use the area without interrupting their feeding activity. In operationalizing this definition a patch was assumed to be a single tree (or under rare circumstances the food trees of the same species with adjoining canopies; this usage is examined below).

It is difficult to count the individual food items remaining in a tree after a primate group has left it. Thus, for the purpose of this investigation, patch depletion was inferred from the actions of individual monkeys. Their behaviour was monitored in situations where their actions could be predicted if they were depleting the patches in which they fed. For example, if a primate group was depleting a food patch, the acquisition of food items per individual in a patch should be negatively related to the time the group has spent in the patch. Also, the time the study group spends in a patch will be a function of the size of the patch and the number of individuals in the group (i.e. if depletion occurs large groups should stay in equally sized patches for less time than small groups and small patches should be left sooner than large patches). Theoretically, a patch may be considered depleted when the feeding activities of consumers have led to the disappearance of all food items (Cant and Temerin 1984). However, once food items become rare within a tree, they become progressively harder to obtain, and thus a patch will be functionally depleted before all of the

food items are eaten. From this perspective, patches have been considered depleted when the rate of intake of items in a patch equals the average of the environment (Charnov 1976, Pyke 1984).

Methods

The study was carried out in Santa Rosa National Park, Costa Rica during four field seasons encompassing 24 months (July and August 1983, January to August 1984, January to July 1985, and February to August 1986). In the last season only spider monkeys were studied. Rectangular in shape and covering approximately 10,800 ha, Santa Rosa consists of a series of plateaus which start at an elevation of 300 m and drop to the ocean. The vegetation of the park is a mosaic of grassland (Hyparrhenia rufa), dry deciduous forest in which Spondias mombin, Luehea candida, L. speciosa, Guazuma ulmifolia, Bursera simaruba, and Chlorophora tinctoria are common, and small fragments of semi-evergreen forest containing Hymenaea courbaril, Mastichodendron capiri, Castilla elastica, and Manilkara chicle (Bonoff and Janzen 1980, Janzen 1986, Chapman unpublished data).

The howling monkey study group consisted of 40 individuals; 7-8 adult males, 16-18 adult females, 1-2 large immature males, 1 large immature female, 4-6 small immatures, and 6-9 infants. An exact count of the size of the spider monkey community was not possible, because of the fission-fusion type of social organization exhibited by spider monkeys. However, a minimum estimate of the size of the community was obtained by summing the maximum counts of all age/sex classes seen in any one year. Using this method the community was estimated to consist of 42 individuals; 4 adult males, 17 adult females, 2 large immature males, 4 large immature females, 7 small immatures, and 8 infants.

Behavioural Sampling

Behavioural data were collected using a focal animal sampling regime with 10 minute sessions (J. Altmann 1974). When possible the subject chosen for sampling was selected according to a fixed rotation between age and sex classes. Normally, the species chosen to be sampled was alternated each day. Also, an attempt was made to obtain a complete record of

each species' activity during a 3-week sample period so that at the end of each period an equal number of observations were made in each hour of the day. Using this sampling regime, 394 hours of focal animal data were collected on the howling monkey group and 335 hours on the spider monkeys. Whenever all food items handled by an individual could easily be seen, counts were made of the rate of ingestion. The Diameter at Breast Height (DBH) of the trees used by the monkeys was estimated visually (error in estimation of DBH was ±1.6 cm, n=46, mean DBH of trees used was 43.1 cm for spiders and 62.6 cm for howling monkeys).

Both the spider and howling monkey groups frequently formed subgroups. The members of a subgroup tended to coordinate their activities, maintain relatively close spatial contact, and be spatially discrete from other subgroups. This type of association was similar to that typically described for spider monkeys, but was a radical departure from the relatively stable cohesive social groups typically described for howling monkeys (Chivers 1969, Estrada 1984, Glander 1980, Milton 1980, Smith 1977). The howling monkey study group frequently fragmented into 2 or more subgroups that were spatially separated by up to 2 km, for periods that lasted as long as 4 weeks. The howling monkeys were in subgroups, rather than in a single group, for 84% of the time. The spider monkey subgroups changed composition approximately every 2.0 hours. The howling monkey subgroups were more stable and changed composition every few days as animals (primarily males) moved between subgroups. To determine the size and composition of howling monkey subgroups, counts were normally made once each time a subgroup was observed and the composition was assumed to be stable over the period of observation. Since the location and size of all howling monkey subgroups were usually known, a count of any single subgroup was thought to be accurate since the sum of all subgroups closely approximated the total group size. In an effort to obtain an accurate estimate of the size of spider monkey subgroups, whenever a subgroup was sighted the immediate area was searched for unseen animals. Also, only subgroups that were followed for more than 30 minutes were used in the following analyses. Inactive and unseen individuals would likely have been seen prior to the end of that time.

Ecological Sampling

To determine the size and distribution of the food resources eaten by each species, the most commonly used plant species were determined from the preceding 3 weeks of behavioural observations, and the location, size, and phenological status of all adult trees of these species were determined in three 4-hectare grids. Each grid was 200 m by 200 m and consisted of 400 cells, each 10 m by 10 m in size. Corners of the cells were marked with steel posts. An adult tree was considered as any individual tree with a DBH greater than the smallest individual seen to bear fruit. The size of a patch would ideally be represented as the number of food items it contained; however, the large number of patches used by both of these species precluded the counting of food items, so patch size was represented by DBH. Several previous studies have demonstrated that DBH accurately predicts the reproductive capacity of fruiting individuals for a number of tropical tree species (Leighton 1982, Leighton and Leighton 1982, McDiarmid et al. 1977 Peters et al. in prep). The phenological information recorded involved assessing the stage of leaf development and noting the presence or absence of fruit and flowers. In 1984, phenological data were recorded on the major plant species used by either of the monkey species during the preceding 3 weeks of behavioural sampling. In 1985 and 1986, the phenological status of all individuals of all major plant species used by either the howlers or spiders any time during the study were assessed. When a plant species was used that had not been eaten in the past, phenological data were recorded for it in all subsequent ecological sampling periods.

A 3-week sampling period was chosen because within this period an adequate sample of each species' behaviour could be obtained and the phenological cycles of the majority of the food plants used by the monkeys bore food items for over 3 weeks; thus individual trees possessing food items at the beginning of a 3-week period usually possessed them at the end of the sample period. Individuals of the few species of plants that were exceptions to this rule (e.g. flowering Tabebuia ochracea) could be identified by looking for food items that had fallen to the ground. Thus, food resources were not so ephemeral that they could not be accurately sampled in a 3-week period or that the two primate species could not respond to the changes.

The distribution of all variables used were examined for normality, and when values were not normally distributed an appropriate transformation was applied. The reverse transformations were corrected for bias (see Beauchamp and Olson 1973, Millar 1984).

Results

Does a Tree Equal a Patch?

To determine if the resources used by these primates can be considered to occur in patches and whether or not it is a typical situation for one tree to represent a patch, the time spent moving between food trees (excluding rest stops) was determined for each instance where a subgroup was followed from one tree to another. This sampling procedure tended to bias the sample in favour of short movement because subgroups were more likely to be lost or abandoned during long movements. For spider monkeys the average time spent moving from one food tree to another was 703 seconds (range = 5 to 3660 seconds, in 172 movements). Less that 15% of these movements were less than 1 minute in duration and of these short bouts 76% involved foraging bouts occurring in one area with a number of Muntingia calabura trees growing close together. In 90 observed movements of howlers, the average time spent moving between food trees was 402 seconds (range from 10 to 1421 seconds, 24 minutes). Less than 13% of these movements involved bouts of less than 1 minute. Spider monkeys spent significantly more time moving between food patches than did howlers ($t=3.5$, $P=0.032$). Relative to the time spent moving between trees, both species tended to have movements of short duration within a tree (94% of the movements made by howlers within a tree were less than 30 seconds, 97% of the spider movements within a tree were less than 30 seconds).

To further examine this assumption, the grid location of all individuals of the major food plant species was determined in all of the sample periods for both of the monkey species. Many of the resources used by both species (e.g. Ficus sp., Swartzia cubensis, Mastichodendron capiri) occurred at low densities (Appendix 1:3). Resources occurring at low density tended to be spatially separated and thus an individual tree was likely to represent a

patch. The average density of the food plants that were used by the howling monkeys for greater than 1% of their feeding time was low (7.96 trees/ha) and 63% of these plant species occurred at a density of less than 1 individual per hectare. Similarly, food plants constituting greater than 1% of of the spider monkey's feeding time were found at an average density of 4.76 individuals per ha and 52.9% of these species occurred at a density of less than one individual per hectare. For both species it was common for only 1 individual food bearing tree of a particular species (e.g. Ficus sp., Swartzia cubensis) to occur in the 12 ha gridded area.

Foraging Behaviour As Related to Patch Use

The howling monkeys studied in Santa Rosa were primarily folivorous. They spent 49.0% of their feeding time eating leaves, compared to 28.5% and 22.5% of their feeding time eating fruit or flowers, respectively. In contrast, spider monkeys spent 77.7% of their feeding time eating fruit, and patches containing fruit represented 88.0% of the total number of patches visited. Feeding on flowers and leaves constituted 9.0% and 11.9% of the spider's feeding time, respectively.

On average, spider monkeys spent 810 seconds feeding in a patch they visited (range = 10 - 5021 seconds, n=147). The time spent in a patch did not differ between the type of patch being used. Spiders on average used flower patches for 729 seconds (n=13), and used patches containing fruit (n=121) or leaves (n=13) for 814 seconds and 853 seconds, respectively ($F=0.0580$, $P=0.9431$). The time spent in a patch was related to the season; spiders spent significantly less time in each patch visited in the dry season (mean = 643 seconds, n=78) than in the wet season (mean = 999 seconds, n=69, $t=2.17$, $P=0.032$). Howling monkeys spent an average of 1275 seconds in a patch (n=78), which tended to be a longer period than that of spider monkeys ($t=1.87$, $P=0.068$). The time that howlers spent in a patch did not differ between the type of patch they were using (fruit 1638 seconds n=44, flower 684 seconds n=24, leaves 906 seconds n=20, $F=1.397$, $P=0.262$). The howlers spent longer in patches in the dry season (mean = 30.1 minutes) than in the wet season (mean = 12.9 minutes, $t=7.927$, $P<0.001$).

The average DBH of the food trees used by spider monkeys was 43.1 cm with a range of 7 cm to 185 cm. The patches used to obtain flowers had on average the largest DBH (mean DBH = 56.6 cm, n=13), followed by fruit patches (mean DBH = 37.8 cm, n=121), and leaf patches (mean DBH = 33 cm, n=13), but these differences were not significant ($F=0.651$, $P=0.438$). Although, time spent feeding in patches showed seasonal variability, patch size showed no significant change with season (mean patch size, dry season 39.2 cm DBH n=79, wet season 47.0 cm DBH n=69, $t=1.39$, $P=0.167$). The howling monkey group used patches with an average DBH of 62.6 cm, which was significantly larger than the size of the patches used by the spider monkeys ($t=3.39$, $P<0.001$). The average size of the different types of food patches used by the howlers was similar (fruit, mean DBH = 63.8 n=44; flowers, 63.9 n=24; leaves, 59.0 n=20). Unlike spiders, the size of the patches used in the wet season by the howlers (mean DBH = 79.4 cm n=34) was significantly larger that the size of those used in the dry season (mean DBH = 44.9 cm, n=54, $t=22.4$, $P<0.001$).

Do These Primates Deplete The Patches They Use?

One line of evidence suggesting that both spiders and howlers generally deplete the trees they use in a single visit is that they were frequently observed to feed in a number of individual trees of the same species in direct succession. This occurred even if the individual trees were far apart. For instance, spider monkeys on average spent 821 seconds moving between different individual Sloanea terniflora trees, and it was not uncommon for them to visit four or five different trees in direct succession. One explanation for these observations is that the monkeys were feeding in a tree and depleted its food resources to a level where it was more profitable for the animals to travel to a new tree where presumably the rate of intake of food items would be higher than if they remained feeding in the original tree. Other explanations for the observed pattern, such as a need to travel in order to adequately defend territorial boundaries, cannot be ruled out by these observations.

A second line of evidence of patch depletion is that for most tree species the rate of intake of food items during a feeding bout in a single patch was higher at the start of the feeding bout than later in the same feeding session (paired t-test howlers $t=5.51$, $P=0.005$,

spiders $t=4.32$, $P<0.001$, average length of feeding session for spiders was 810 seconds and for howlers 1275 seconds). One possible interpretation of this result is that food items are easier to find when a subgroup first enters a tree than after they have been feeding in it for some time. An alternative explanation for the decrease in the number of food items obtained over the duration of the feeding bout is that the animals are becoming satiated. If this explanation were true one might expect a decrease in the rate of acquiring food items obtained with all types of plants. However, that was not the case. For instance, the rate of intake of leaves eaten by howling monkeys did not change over the length of a feeding bout ($t=0.780$, $P=0.717$, $n=20$), nor did the rate of intake of fig fruit by spider monkeys decrease ($t=0.39$, $P=0.359$, $n=17$), but the rate of acquiring other fruits by spiders, such as Bursera simaruba ($t=11.0$, $P=0.029$, $n=23$), Muntingia calabura ($t=9.00$, $P=0.035$, $n=17$), or Dipterodendron costaricensis ($t=6.43$, $P=0.012$, $n=12$) did change over the length of the feeding bout.

An alternative method of assessing the validity of the patch depletion assumption is to assume that primates deplete patches and examine relationships that should be true if the assumption of patch depletion were correct. For instance, if patches were depleted by primate exploitation, larger groups should spend less time than smaller groups in patches of equal size, and thus individuals in a larger group should have to travel farther to obtain their daily ration. Consequently, individuals in large groups might spend more time feeding per day than individuals in small groups to compensate for the added energy expended in travel. There was a significant positive correlation between subgroup size and the time spent travelling for both howlers ($r=0.4829$, $P<0.001$) and spiders ($r=0.461$, $P=0.027$). Similarly, there was a significant positive relationship between subgroup size and the amount of time spent feeding for howlers ($r=0.491$, $P<0.001$) and spiders ($r=0.565$, $P=0.007$). An alternative explanation for this relationship is that members of large subgroups obtain fewer items per minute, possibly associated with increased interference. For both primate species in Santa Rosa intake rate was not related to subgroup size (howler $r=0.197$ $P=0.250$; spiders $r=0.054$, $P=0.417$), so members of differently sized subgroups obtained food items at approximately the same

rate.

If patches were depleted by primate use, one would expect that the time spent feeding in a patch would be a function of the size of the patch and the number of animals using the patch, such that equal sized groups would spend more time in large patches than in small patches, and small groups would spend more time in a patch of a given size than would a larger group. A multiple regression to predict the time that spiders spent feeding in a patch from the size of the patch (all types of trees) and the number of individuals feeding in the patch produced a significant relationship (R^2=0.421, P<0.001, log time in a patch = 1.11 + 1.11 log patch size - 0.25 log subgroup size). The relative influence of these two variables on the time that spider monkeys spent in a patch can be assessed in a number of ways. A partial correlation analysis of feeding time versus patch size and the number of individuals using the patch suggests that the size of the patch has a stronger influence on the time spent in a patch than does the number of individuals using it (log transformed feeding time versus patch size, controlling for subgroup size, r=0.644, P<0.001, feeding time versus subgroup size, controlling for patch size, r=0.151, P=0.028). A more precise means to show the relative influence of the dependent variables on the time the spider monkeys spent in patches, which shows the actual data used, is to construct standardized partial regression plots (Figures 1,2). Comparing the scatter in Figures 1 and 2 illustrates that the influence of patch size on feeding time is stronger than the influence of subgroup size on feeding time in a patch.

For howling monkeys, using all types of patches, the size of the patch and the number of animals feeding within the patch explained little of the variation in the time spent feeding in a patch (R^2=0.093, P=0.860, log of time in a patch = 2.27 - 0.31 log subgroup size + 0.55 log patch size).

It is possible to examine what types of patches are depleted by primate use. Although the time howlers spent feeding in all types of patches could not be predicted well by patch size and the size of the subgroup, if only fruit patches are used in this analysis, the relationship is significant (R^2=0.333, P=0.011, log of time in a patch = 1.00 + 1.46 log patch size - 0.46 log subgroup size). The relative influence of these variables on the time howling monkeys

spent in patches was assessed in two ways. In a partial correlation analysis both the number of individuals using a fruit patch and the size of the patch were significantly related to the amount of time spent feeding in that patch (partial correlations of feeding time versus patch size controlling for subgroup size log transformed $r=0.577$, $P=0.002$; feeding time versus subgroup size controlling for the size of the patch, $r=0.267$, $P=0.050$). By plotting the standardized partial regressions, the data can be presented and the relative influence of each dependent variable on the time spent in a patch when the other dependent variable is held constant (Figures 3,4).

In contrast to when howlers fed on fruit, when they fed on leaves, patch size and the number of individuals in the subgroup did not predict feeding time in the patch ($R^2=0.249$, $P=0.366$, log of time in a patch = 4.61 - 0.69 log patch size - 0.51 log subgroup size).

Different subgroups of spiders occasionally used large fruiting trees soon after they were abandoned by a previous subgroup, or one subgroup would return to a large fruiting tree repeatedly throughout the day (e.g. Ficus sp.). These observations suggest that large fruiting trees may not have been depleted by the spider monkeys. A multiple regression of the time in a patch versus patch size and subgroup size were conducted using only trees of specific size. This relationship became non-significant once only trees with a DBH greater than 60 cm were used (log transformed >60 cm $R^2=0.103$, $P=0.135$, <60 cm DBH $r^2=0.408$, $P<0.001$). This suggests that trees larger than 60 cm DBH were not depleted by spider monkeys. Trees with a DBH larger than 60 cm only accounted for 20.5% of the patches that spiders visited and 36.5% of these occurred in one sample period. Similar to howlers, the depletion of patches by spider monkeys was a function of the type of patch they used. When spiders fed on leaves, the time they spent in a patch could not be predicted by its size and the size of the subgroup using it (log transformed leaves $R^2=0.052$, $P=0.389$). However, when spiders fed in fruit or flower patches the multiple regressions were highly significant (flowers $R^2=0.705$, $P=0.007$, log of time in a patch = 0.53 + 1.60 log patch size - 0.37 log subgroup size, fruit $R^2=0.448$, $P<0.001$, log of time in a patch = 1.08 + 1.13 log of patch size - 0.27 log subgroup size).

The question of when patches are depleted can be asked for each tree species that the spiders used by examining if the time a subgroup spends in a patch can be predicted from the trees size and the subgroups size. However, since many of the trees the spiders used were found at a low density, there was little variation in the size of the patch for many tree species, and thus the number of tree species for which this multiple regression can be examined is small. The time that spiders spent in Sloanea terniflora (R^2=0.554, P=0.030, n=10), Bursera simaruba (R^2=0.455, P=0.011, n=23), and Muntingia calabura trees (R^2=0.391, P=0.020, n=17) was related to the size of the tree and subgroup size, but for Ficus sp. (R^2=0.121, P=0.216, n=17) and Dipterodendron costaricensis (R^2=0.009, P=0.480, n=12) that relationship was not significant.

Discussion

For both species, an increase in the time spent travelling associated with membership in large subgroups corresponded closely to an increase in feeding time. That suggests that animals may attempt to obtain a constant amount of energy after varying expenditures are accounted for. Large subgroups may spend more energy on travel, but ingest more over the course of the day, so that the energy gained minus the energy expended is the same regardless of subgroup size. If these primates attempt to reach a certain net energy level every day, both the amount of food in a patch and the distance between patches, could set the optimal group size to maximize feeding efficiency.

I used the multiple regression equation of feeding time in a patch versus patch size and the number of individuals using the patch, and set patch size to the average, to calculate the expected feeding time of subgroups of different sizes (for howlers only fruit patches were used). This procedure simulates the effect of repeatedly adding members to a feeding subgroup and reveals that the effect on feeding time of adding an additional member is greater for small subgroups than for large subgroups (Figure 5). This trend could result from an exponential increase in interference as subgroup size increases. Klein (1972) observed that when a spider monkey subgroup fed in a tree, all members were dispersed evenly throughout

the canopy, and when one member moved to a different location, the other members tended to move to maintain equal spacing. This cost of repeatedly maintaining personal space would increase dramatically in a large subgroup. Thus, in larger subgroups where interference is high, animals would not deplete the patches as rapidly as they would if there was no interference, for they repeatedly spend time avoiding conspecifics that would otherwise be spent eating. This tendency would result in the group staying in the patch longer than predicted based on the size of the patch. A number of researchers have found a relationship between the level of aggression and the size of the patch. Waser (1977) found increased aggression in small patches as the size of mangabey groups increased. Similarly, Klein and Klein (1977) found an increase in aggression when spider monkeys fed in small trees, and Chivers (1977) observed the same relationship with siamangs. Sussman and Richard (1974) found that lemurs were aggressive when food occurred in limited areas. However, for the spider monkeys of Santa Rosa there was no relationship between agonistic behaviour and patch size ($r_s = 0.112$, $P = 0.210$).

By substituting the average patch size and subgroup size into the same regression equation, the average feeding time can be calculated. Subsequently, the effect of different patch sizes on the expected feeding gain with subgroup size held constant can be calculated, and vice versa (Figures 6A,7A). Feeding gain was calculated in this fashion to construct a relative scale, so that the values above zero represent a gain in feeding time above the average time that was normally spent in a patch, and negative values represent feeding bouts of shorter duration than the average. These calculations illustrate that the advantage of feeding increases almost linearly with patch size for both howlers and spiders. This demonstrates one advantage of selecting large trees. In contrast, the effect of subgroup size on feeding advantage is not linear for either species. Figures 6B and 7B illustrate that for both species, there is a substantial feeding advantage to an individual if it feeds in a small group or as a solitary animal. Since most primates do not forage alone, this relationship implies that the advantages of living in a group, such as social advantages or protection from predators, are substantial.

By comparing the point at which the curve, depicted in Figures 6B and 7B, intersects the ordinate for howlers and spiders, provides some clues as to why spider monkeys have a social system so atypical for a primate. For spiders the feeding gain of very small subgroups was relatively less than the feeding gain of small howling monkey subgroups. Thus, a spider monkey stands to gain a larger feeding advantage by being in a small subgroup than would a howling monkey. For instance, when spider monkeys are feeding in average sized patches, foraging costs, such as travelling between patches, will equal feeding benefits when 9 animals are in a subgroup. In contrast, for howling monkeys, costs will not equal benefits under these conditions until 20 animals are in a subgroup. Ignoring other possible influences on group size, this finding suggests that to forage efficiently, spider monkeys should be in smaller subgroups than howling monkeys.

This study suggests that howling and spider monkeys use resources that occur in patches and deplete many of the patches they use, particularly fruit patches. The decision of when to leave a patch should be a function of the rate at which the patch is depleted, relative to the availability of other patches (Charnov 1976, Pyke 1984, Krebs 1979). Depletion rates will be strongly influenced by the number of co-consumers using the same patches. In tropical ecosystems a large number of species frequently use the same resources (Fleming 1979, Rockwood and Glander 1979). For instance, Willis (1966) observed 28 Columbian bird species using a single plant.

Since deciding when to leave a patch is a function of the animals perception of the availability of alternative food sources, it will also be related to the species' ability to sample their environment. A number of researchers have stated that there are striking regularities in many aspects of primate ranging behaviour (Clutton-Brock 1975, Nishida 1968). Regular movements may serve as a means of systematically sampling the environment. Sampling ability may be highly variable between species. The two species studied here had very different strategies of sampling. The spider monkeys used resources that appeared were relatively ephemeral in comparison to the howlers. The longer day ranges of the spiders may represent their attempt to sample the environment. Also, the sleeping trees of the spider monkeys,

which were used at night by the subgroups that had been foraging separately throughout the day, may serve as "information centers" as proposed by Ward and Zahavi (1973) for colonial birds. Since these primates generally deplete the patches they use, and since the patches they use are relatively discrete and easily located, they may prove to be good subjects for the investigation of sampling behaviour.

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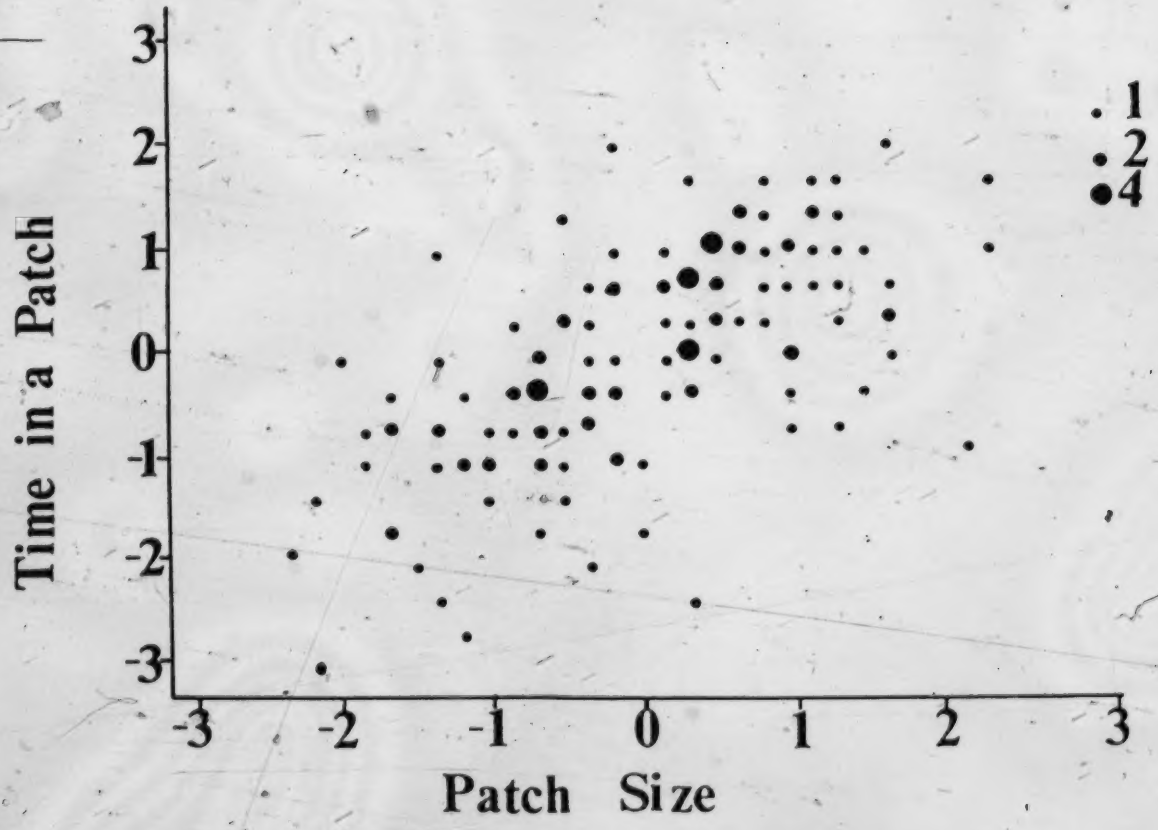

Figure 1.

A standardized partial regression plot which expresses the influence of the size of the patches used by the spider monkeys of Santa Rosa National Park, Costa Rica on the time spent in patches when the subgroup size is held constant. This analysis uses all types of trees.

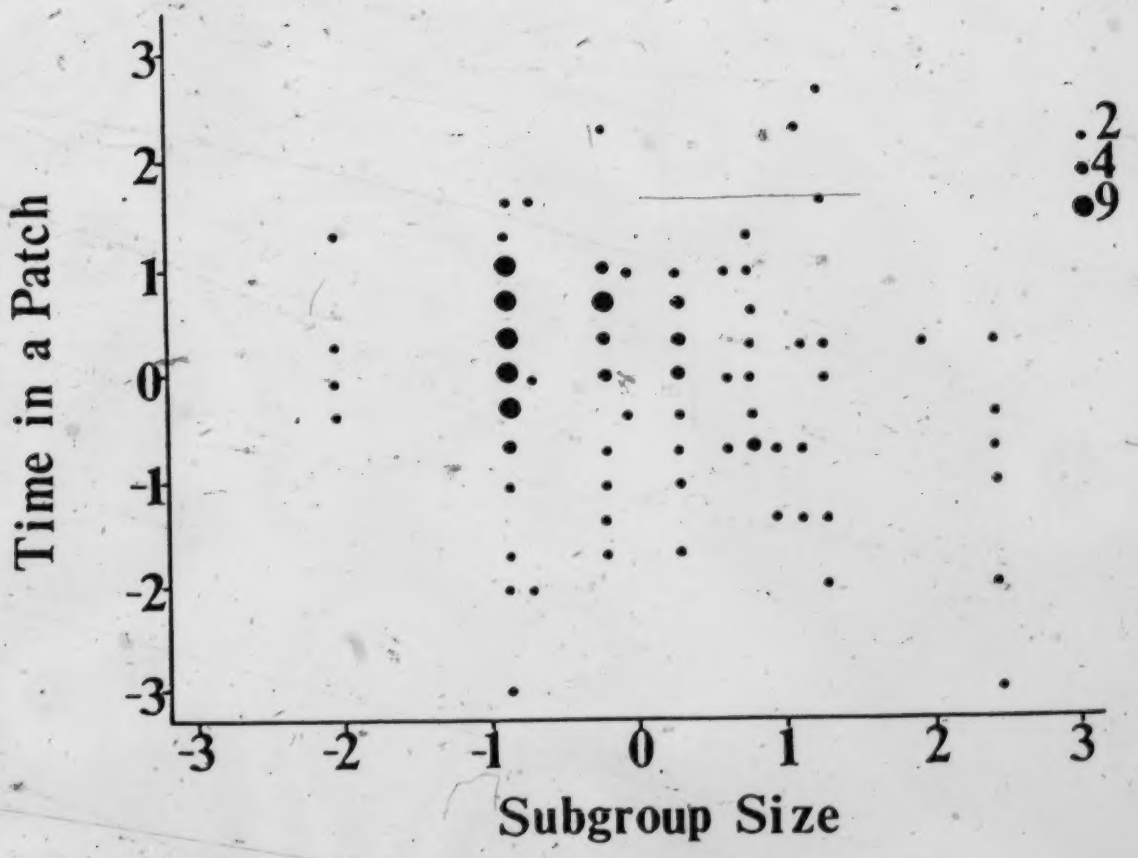

Figure 2.

A standardized partial regression plot which expresses the influence of the size of the subgroup of the spider monkeys of Santa Rosa National Park, Costa Rica on the time they spent in patches when the size of the patch is held constant. This analysis uses all types of patches.

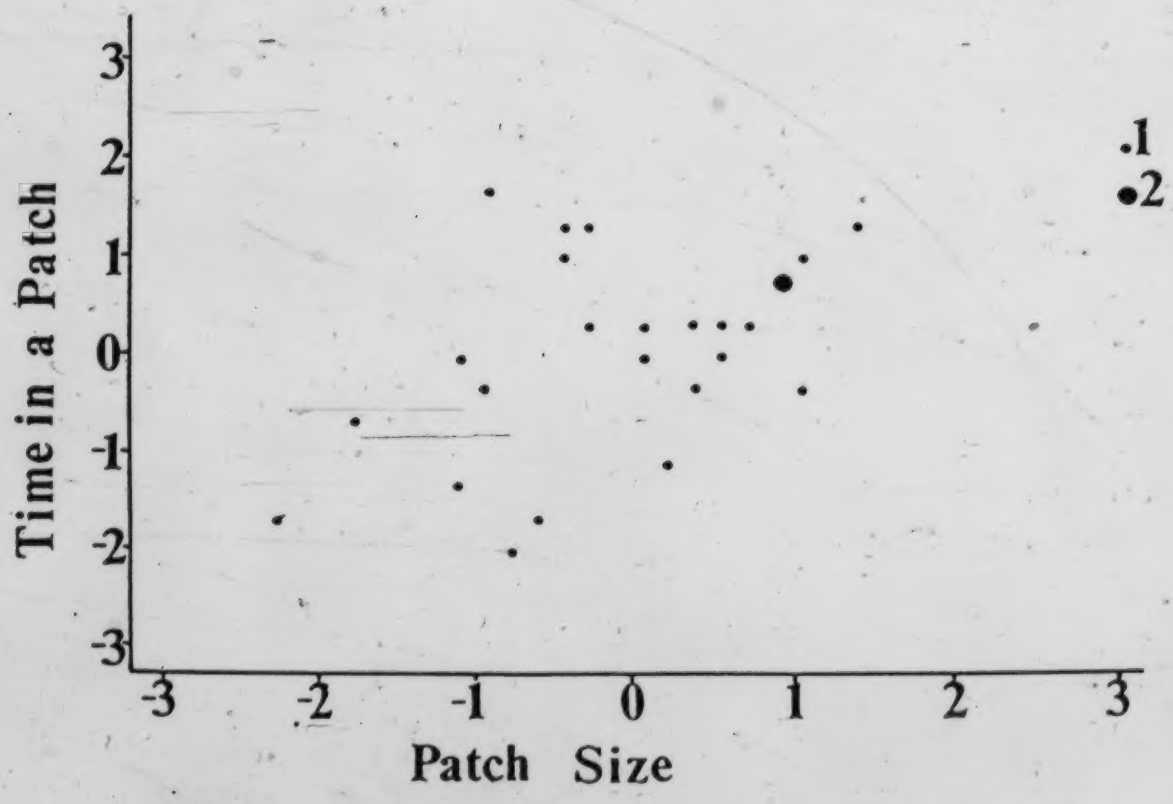

Figure 3.

A standardized partial regression plot which expresses the influence of the size of the patches used by the howling monkeys of Santa Rosa National Park, Costa Rica on the time they spent in patches when the subgroup size is held constant. This analysis uses only the fruiting trees used by the howling monkeys

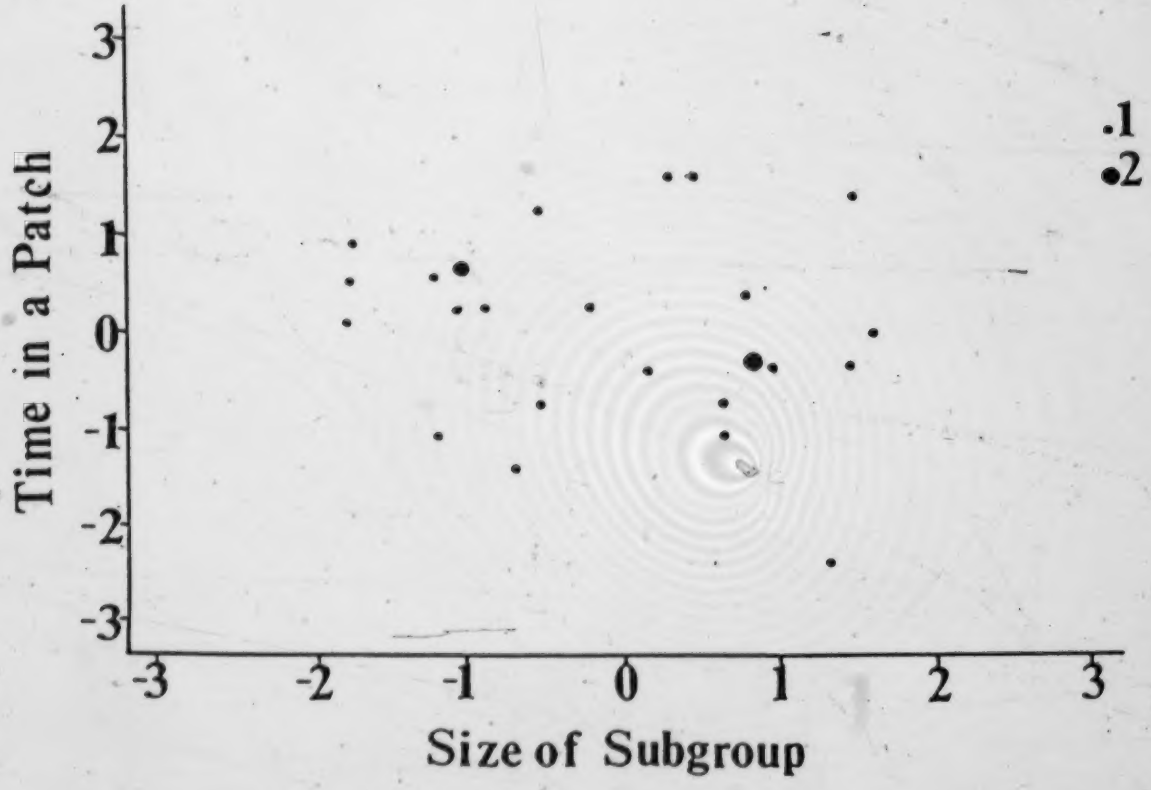

Figure 4.

A standardized partial regression plot which expresses the influence of the size of the subgroup of the howling monkeys of Santa Rosa National Park, Costa Rica on the time they spent in patches when the size of the patch is held constant. This analysis uses only the fruiting patches used by the howling monkeys.

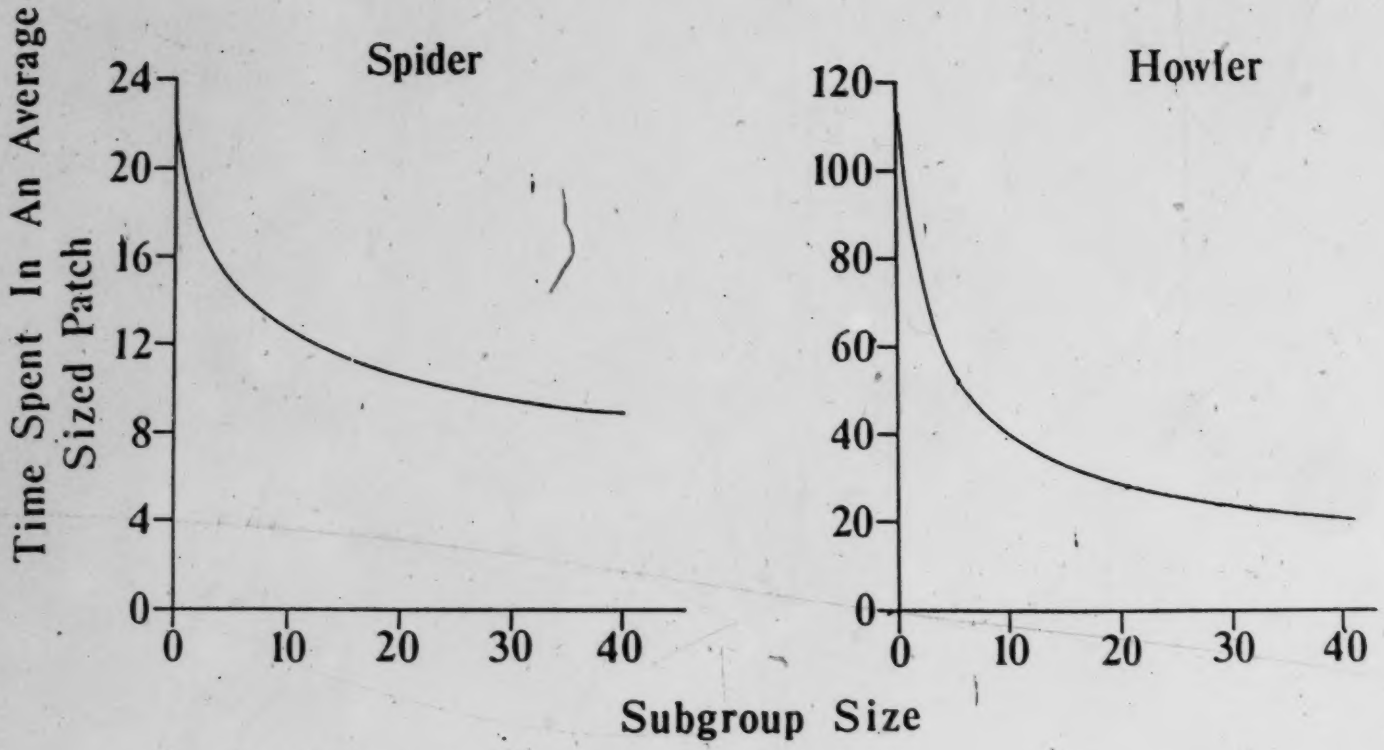

Figure 5.

For the spider and howling monkeys of Santa Rosa National Park, Costa Rica the effect on expected feeding time of adding group members to a subgroup was simulated by using a multiple regression equation of feeding time versus the patch size and the size of the subgroup and setting patch size to the average.

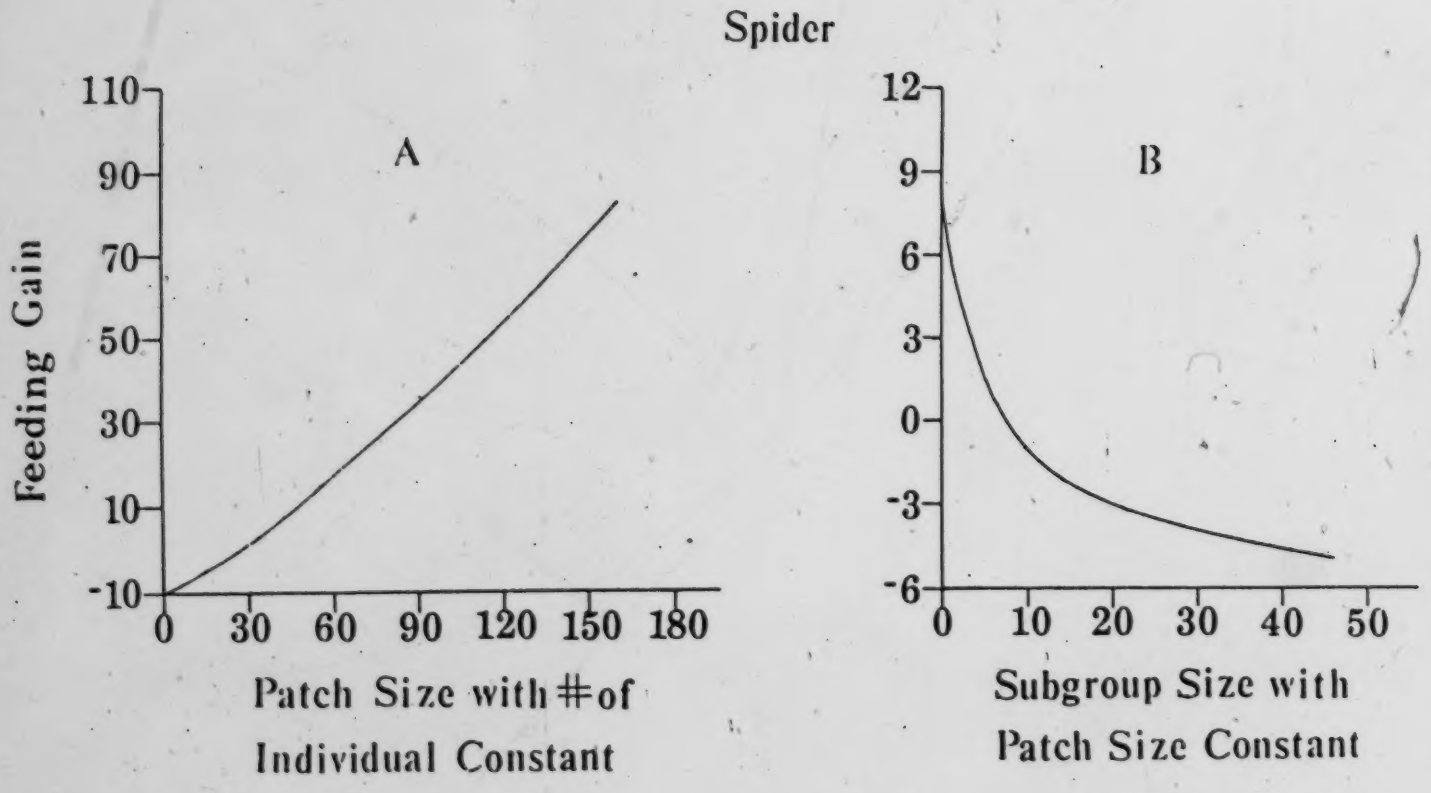

Figure 6.

For the spider monkeys of Santa Rosa National Park, Costa Rica the average feeding time was calculated first with subgroup size held constant and then with patch size held constant, from a multiple regression equation of feeding time versus the patch size and the size of the subgroup using the patch.

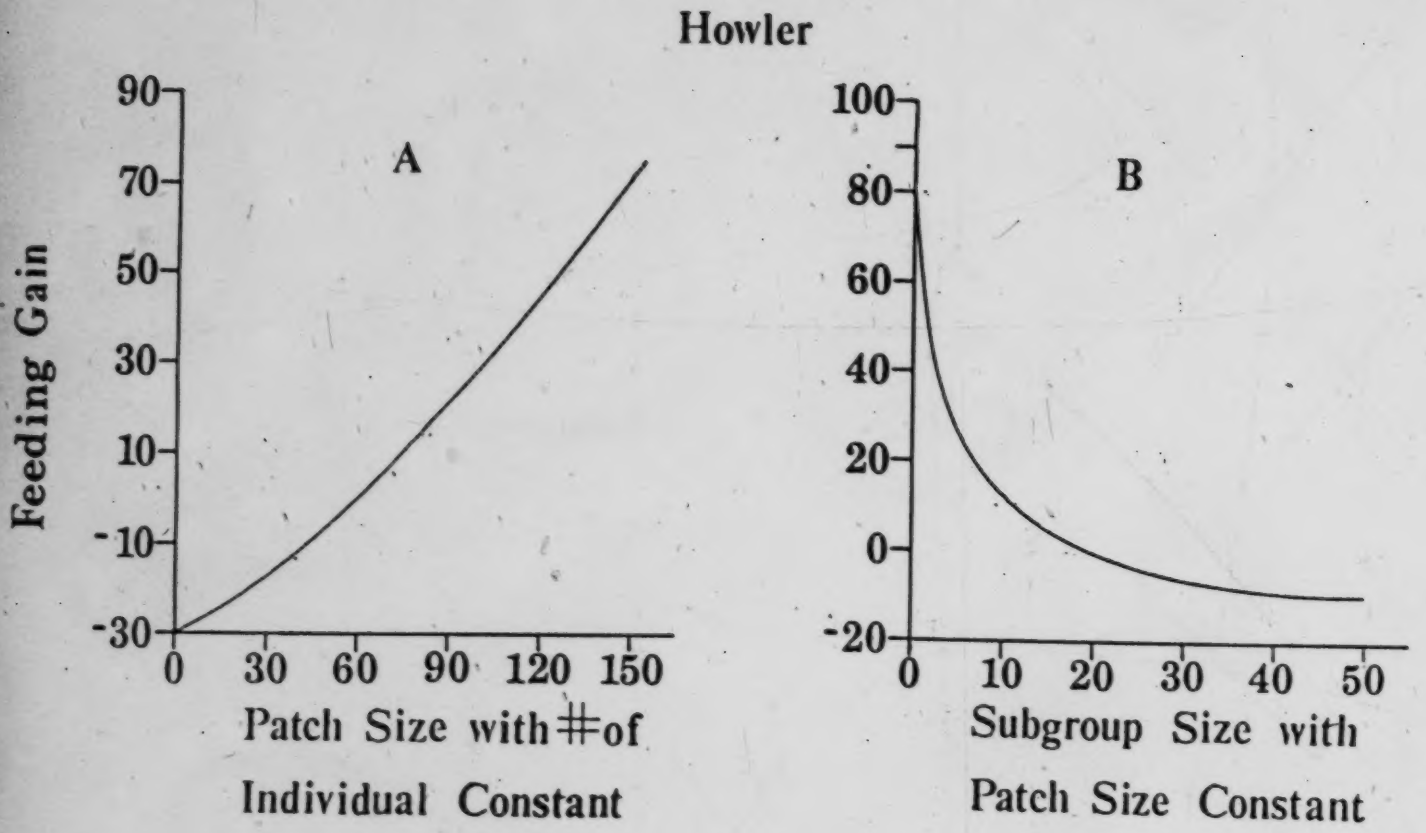

Figure 7.

For the howling monkeys of Santa Rosa National Park, Costa Rica the average feeding time was calculated first with subgroup size held constant and then with patch size held constant, from a multiple regression equation of feeding time versus the patch size and the size of the subgroup using the patch.

IV. Flexibility in Diets of Three Species of Costa Rican Primates

Introduction

Recent evidence from long term studies of primates indicates that many species have highly varied diets and show considerable flexibility in the types of food items eaten (Hladik 1977, Lindburg 1977, MacKinnon and MacKinnon 1978, 1980, Milton 1980, 1984, Oates 1977, Richard 1977, Struhsaker 1975, Waser 1977). For instance, MacKinnon and MacKinnon (1980) found that the percentage of fruit in the diet of Presbytis obscura varied between months from 13% to 80%.

Studies conducted over a number of years have discovered striking dietary differences between years (Hladik 1977, Kinzey 1977, Struhsaker 1975, Waser 1975,1977). Waser (1977) provided a number of examples of annual variation in the dietary patterns of Cercocebus albigena. For instance, he observed mangabeys feeding on the leaves of Platycerium in 1971 but not again until 1974, yet leaves were available in the intervening years. Similarly, Struhsaker (1975) found major differences in what was eaten by Colobus badius in the same months in different years.

Intraspecific dietary differences between primate groups observed at different locations have been demonstrated in a number of field studies (Clutton-Brock 1974, 1977, Hladik 1977, MacKinnon and MacKinnon 1978, 1980, Oates 1977, Richard 1977, Struhsaker and Leland 1979, Waser 1977, Wrangham 1977). The majority of these dietary differences were likely a result of differences in what was available at the study sites. However, dietary differences found between some populations cannot be explained by availability (Hladik 1977, Kawamura 1959, Azuma 1973, Richard 1977, Struhaker 1975, Waser 1977). Richard (1977) found that one population of Propithecus verreauxi fed extensively on the fruits of Rothmannia decaryi, while another population ignored the fruit. Such variability in diet could influence both how primates interact with their environment (e.g. seed dispersal, Herrera 1985) and how they interact with other species (e.g. competitive interactions, Strong 1983,

Wiens 1977).

The objective of this study was to examine the degree of flexibility in the diets of the three species of primates (Ateles geoffroyi, Cebus capucinus, Alouatta palliata) living in Santa Rosa National Park, Costa Rica by analysing how their diets vary between months and between years. In addition, I attempted to discern the effect of this variation on the dietary overlap between the primate species to provide insights into how dietary overlap may have influenced the development of feeding strategies.

Methods

The study was conducted at Santa Rosa National Park, Costa Rica during four field seasons; July and August 1983, January to August 1984, January to July 1985, and February to August 1986. In the last year only spider monkeys were observed. Santa Rosa is a 10,800 ha National Park, situated 35 km northwest of Liberia, adjacent to the Pan-American Highway. The climate of the region is very seasonal, with a dry season beginning in mid December and ending in late May and a wet season encompassing the rest of the year. Rainfall ranges between 900 mm and 2400 mm annually. As a result of natural topography and past land use practises, the vegetation of the park is a mosaic of grassland (Hyparrhenia rufa), dry deciduous forest containing Spondias mombin, Luehea candida, L. speciosa, Guazuma ulmifolia, Bursera simaruba, and Chlorophora tinctoria, and semi-evergreen forest containing trees such as Hymenaea courbaril, Mastichodendron capiri, Castilla elastica, and Manilkara chicle (Bonoff and Janzen 1980, Janzen 1982a,b,c, 1986, Chapman unpublished data).

I concurrently studied one group of each primate species to maximize the temporal similarity of the available foods. The study groups occupied home ranges that overlapped extensively and included areas of both dry deciduous and semi-evergreen forest (see Chapter 2). The howling monkey group contained on average 40 individuals, and the cebus monkey group was comprised of 26 individuals. Both groups were large for Santa Rosa, as the mean group size for the park in 1984 was 14.0 animals for cebus monkeys and 13.7 individuals for howlers (Fedigan et al. 1985). The fluid social structure of spider monkeys precluded an

accurate estimate of community size. However, the minimum size of the community was estimated by summing the maximum counts of all age/sex classes seen in any one year. Using this method the community was estimated to contain 42 individuals (Chapman and Fedigan in prep.).

Behavioural data were collected using a focal animal sampling regime (Altmann 1974) which employed a session length of 10 minutes. If the subject was lost prior to the end of the session, the session was terminated and the data discarded. When the focal animal was observed feeding, the species of plant it was eating, the size of the food plant (estimated as Diameter at Breast Height, DBH), and the type of food eaten (i.e. fruit, flower, young leaves, etc.) were recorded. With this sampling procedure, 394 hours of focal animal data were collected on howling monkeys, 335 hours on spider monkeys, and 171 hours on cebus monkeys. Normally the species chosen to be sampled was alternated each day, although this varied somewhat depending on the ease with which each species could be located on a particular day. An attempt was made to obtain a complete record of each species' activity during a 3-week sample period, so that at the end of the period an equal number of observations were made in each hour of the day. A scan sample was taken every half hour in 1984 and every ten minutes in 1985 and 1986 to assess the group's activity, the tree species being used, the trees size (DBH), the height of group members in the canopy, the proximity of other primate species, and the group's location. Location was recorded as a coordinate on a grid (120 m by 120 m) superimposed on an aerial photograph of the group's home range.

To describe the average size and density of the plant species being used by each of the three primates, the most commonly used food resources were identified for each primate species from the preceding 3 weeks of behavioural observation, and the location, size, and phenological status of all adult food trees were determined in three 4-hectare grids. These grids each contained 400 cells which were 10 m by 10 m in size. Corners of the cells were marked with a steel post. The grids encompassed 9% of both the cebus and howling monkey's home ranges (Appendix 1:1B). Each grid was established in slightly different habitats, so that the major habitats used by the monkeys were all sampled. An adult tree was considered as any

individual that had attained a DBH of the smallest individual known to bear fruit. The phenological data recorded involved assessing the stage of leaf development (i.e. no leaves, leaf buds, young leaves, mature leaves) and noting the presence or absence of fruit and flowers. The size of the trees was represented as DBH which has been shown for a number of tropical plant species to accurately reflect the reproductive capacity of fruiting individuals (Leighton 1982, Leighton and Leighton 1982, McDiarmid et al. 1977, Peters et al. in prep.). Intraspecific dietary overlap between adjacent months and between the same months in different years, and interspecific dietary overlap were calculated using the following formula:

$$D = Si$$

where D = Dietary overlap

Si = % of diet shared between two periods or species

This formula was used by Holmes and Pitelka (1968) in their study of sandpipers and by Struhsaker (1975) in his study of the feeding ecology of red colobus (Colobus badius).

Selectivity for a particular food item was measured as the proportion of the total time spent feeding on that food item divided by the density of the adult trees carrying that food item. Density was determined from counts conducted in the 4-hectare grids and was expressed as the number of individuals per hectare.

Results

The most common means of classifying primate diets is to categorize them from observations made over the total duration of the study, in terms of the proportion of feeding time spent eating different plant parts (e.g. fruit, leaves, etc.). Using this classification system both cebus and spider monkeys were primarily frugivorous, and spent 81.2% and 77.7% of their total feeding time, respectively, eating fruit (Table 1). Howlers were more folivorous than the other two primate species. Leaves constituted 49.0% of their feeding time, whereas fruit accounted for only 28.5% of their feeding time. Cebus monkeys were the most insectivorous of the three species, but the eating of insects constituted only 16.9% of their feeding time.

If each of the three primate species' diets are depicted as the amount of time spent feeding on the different food parts per month, considerable variation is evident (Figure 1). The variability in diet is such that during certain months the cebus monkeys would be classified as largely insectivorous, while in other months they were almost entirely frugivorous. Similarly, the spider monkey's diet varied from being exclusively composed of fruit to being primarily foliage. As shown in Figure 1, the pattern with which diet varied monthly does not appear to be highly synchronized between the species. This was tested statistically for the three types of plant foods using Kendall's Test of Concordance and in no instance did the three species synchronize their feeding (fruit $W=0.210$, $P>0.05$; leaves $W=0.190$, $P>0.05$; flowers $W=0.072$, $P>0.05$).

A more precise means of classifying primate diets is to categorize them in terms of the food items eaten, including the plant species used and the part taken. If the diets of the three primate species studied here are classified in these terms, again there is a large amount of temporal variability in use (Table 2). A quantitative method of comparing the variability in use of the different plant species even when they differ appreciably in their means, is to calculate the "Coefficient of Variation" (CV) (Sokal and Rohlf 1981). For all of the primates species the CV ranges widely among plant species (cebus 83-354, mean=222; howler 163-355, mean=239; spider 95-370, mean=227). Plant items with the lowest CV tended to be those items available for a longer proportion of the study period. However, a number of food items had high CVs even when they were available for the duration of the study, suggesting that the monkeys were not using these plant species in proportion to their availability. Overall no relationship existed between the variability in use of a plant species (CV) and the length of time the resource was available (spiders $r=-0.413$, $P=0.160$; howlers $r=-0.202$, $P=0.438$; cebus $r=-0.486$, $P=0.270$).

Much of the variability in use was likely due to the changing availability of particular food resources. However, that was not the case in a number of instances. For instance, the use of fruits of Muntingia calabura was not related to its availability. Fleming et al. (1985), in a study conducted over 10 years in Santa Rosa, demonstrated that although M. calabura

produces fruits year round, there is a peak in production following the onset of the rainy season. However, in 1984 and 1985 both spider and cebus monkeys fed heavily on M. calabura in the months preceding the rains and greatly decreased the amount of time spent eating this fruit in the months following the rains, the time of the year when the fruits were most abundant. In contrast, before the onset of the wet season in 1986, spider monkeys rarely fed on M. calabura fruits, but they fed on this fruit heavily immediately following the onset of the rains, and continued to use the fruits well after their availability had declined (Appendix 1:5). The consumption of acorns of Quercus oleoides by cebus monkeys and the use of certain mature leaves by howling monkeys are similar examples (Chapman and Chapman in prep.).

It is possible that the variability in the use of resources by the primates was caused by a sampling problem, where the probability of the monkeys finding plants occurring at low densities was largely a matter of chance, and thus the record of use of those plants should be variable. If that were the case, CV in use would be negatively related to the density of plant species. However, contrary to what was speculated, for none of the primate species was the variability in use related to the density of the plant species (spiders $r=0.236$, $P=0.438$; howlers $r=0.170$, $P=0.528$; cebus $r=0.207$, $P=0.756$). Thus, overall variability in resource use was not likely caused by an inability of any of the three primate species to sample their environment.

A means of examining variability in diet, which reduces the effect of availability, is to quantify the dietary overlap between adjacent months (e.g. May vs June and May vs April), since directly adjacent months are likely to have the most similar levels of abundance of particular types of foods (Struhsaker 1975, 1978). For some pairs of months diets were similar, while at other times diets were very dissimilar (Table 3). On average, the diets of the three species tended to overlap by only 31% with a neighboring month. Monthly dietary overlap differed significantly between the species ($F=4.02$, $P=0.030$). An aposteriori comparison demonstrated that the diet of spider monkeys overlapped more between adjacent months than did the diet of howling monkeys (Scheffe's $P<0.05$); cebus were intermediate,

but closer to spiders than howlers. These analyses illustrate that the diets of these monkeys were highly variable, both in terms of the plant parts eaten and the food items (i.e. species part, e.g. fig fruit) used. They also suggest that variability in use was not simply due to the monkeys tracking a variable resource base.

Even though the monthly variability in diet for all three primate species was high, there could be annual consistency in their diets as these three species exploited food resources that became available at roughly the same time each year. When dietary overlap values were calculated for the same month in each of the years that data was available for all three species, little annual consistency in diet between years were apparent (Table 4). In fact dietary overlap calculated between adjacent months was not significantly different from dietary overlap calculated on an annual basis for any of the three species (cebus $t=-0.69$, $P=0.501$, spiders $t=0.40$, $P=0.692$, howlers $t=-0.67$, $P=0.524$). Since the onset of the rains differed between years (May 22, 1984 and May 9, 1985) (Appendix 1:2A) an examination was made of whether or not there was a significant change in dietary overlap if the time frame used for the comparison was shifted by + or - one month (e.g. March 1984 vs April 1985 and March 1984 vs February 1985). This analysis demonstrated that the dietary overlap values obtained from comparisons of the same months in different years was not significantly different from either of the two shifted scales ($F=0.759$, $P=0.385$).

Some of the annual variability in diet was directly related to food resources that were available on a supra-annual basis, such as Mastichodendron capiri and Swartzia cubensis. S. cubensis bears fruit on a supra-annual basis in which several years lapse between fruiting events (D.H. Janzen personal communication). When it fruited in 1985, S. cubensis was used heavily in the months it was available (% of feeding time when available, spiders 6.9%; howlers 11.7%, cebus 9.5%). Mastichodendron capiri bears fruit on a biannual basis, and it constituted as much as 42.2% of the spider monkeys feeding time in a month. When foods such as M. capiri and S. cubensis are not available the monkeys must make alternate dietary selections. Such supra-annual fruiting events induces variability in the diet of these three primate species. However, it seems likely that a large proportion of the annual variability in

diet cannot be related directly to the supra-annual fruiting of specific plants. A number of food items were equally available in all years, but were used heavily in 1 year and little if at all in a subsequent year. For example, the cebus monkey group fed on Quercus oleoides acorns heavily in 1984, while in 1985 no group member was seen eating acorns; yet acorns were abundant in both years. A similar example concerns the use of Bursera simaruba by spider monkeys. B. simaruba is a common tree in areas of dry deciduous forest. In 1984 and 1985, spider monkeys were rarely seen eating this fruit (0.1% of their total feeding time in both years), but in 1986 it constituted 21.8% of their diet in one sample period and 2.4% of their total feeding time that year. This amounted to a 24.5 times increase in the use of B. simaruba between years. The difference in the amount of time spent feeding on B. simaruba cannot be attributed to a change in the availability of the species, since the density of fruiting individuals was similar in each year (individuals/ha 1984,1985 = 20.8, 1986 = 19.7).

Interspecific Dietary Overlap

To assess the consequences of the variability in diets on interspecific dietary overlap it is necessary to calculate overlap in terms of the plant species used and the parts taken. Calculating dietary overlap in this fashion revealed considerable variability in monthly dietary overlap between each pair of the species (range 0-83.7% Table 5). The average monthly overlap was high for cebus-spiders (mean=23.6%) and howlers-spiders (mean=22.9%). However, the range in overlap for howlers-spiders (0-83.7%) was larger than the range for cebus-spiders (0-43.0%). Both the average monthly overlap (mean = 5.0%) ($F=4.39$, $P=0.02$, Scheffe's $P<0.05$) and the range in monthly overlap values (0-30.1%) were lower for the cebus-howler pair than for the other species pairs.

To examine the relationship between the diets of the three primate species, a cluster analysis was conducted in two fashions; first using the proportion of the feeding time that each species spent eating the different plant parts (e.g. fruit, young leaves, etc., Figure 2) and secondly using the six most commonly eaten food items (i.e. species, part) for each primate species (Figure 3). In the first analysis the major clusters were not exclusively formed from the diets of a single species. On four occasions the monthly dietary samples of the

spider monkeys were most closely related to a monthly dietary sample of the cebus monkeys. In one instance a dietary sample of the spider monkeys was more similar to that of howling monkeys than to a different spider monkey dietary sample collected at another time. The monthly dietary samples of the howling monkeys clustered together separate from the monthly dietary samples of the other two primates in all but one case.

The second level of analysis, using the plant species and part, is a more precise level of examining dietary overlap, than examining the different plant parts eaten. The dendrogram produced from this analysis shows little clustering of monthly dietary samples in terms of either monkey species or sample period. Contrary to the first analysis, most dietary samples of howling monkeys were not closely associated. Also, as in the previous analysis, there was no clear seasonal or annual structuring to the dendrogram.

In order for the three primate species to be in a position where competition for resources might occur, they must overlap spatially and use areas at the same time, or at some time interval after one another that is shorter than the time required for the resources to be replenished. The home ranges of the cebus and howling monkeys overlapped considerably (Figure 4). There was a 81.3% overlap in the home ranges of these two primate species. Their core areas overlapped by 66.7%, and the core areas of each of the primate species was used by the other species at some time during the study. For cebus monkeys only 13.7% of the total number of sightings (n=225) were in one of the 120 m by 120 m cells not used by the howling monkey group. Conversely, 19.7% of the total number of sightings (n=314) of howlers were in cells not used by the cebus monkey group. The likelihood of howlers having exclusive use of an area is probably lower than is represented here, because they also overlap considerably with neighboring groups of cebus monkeys. The area that the howling monkey study group used but that was not used by the cebus monkey study group was in an area where a neighboring cebus monkey group was frequently seen (22 occasions).

Since the spider monkeys do not form cohesive groups, home range parameters cannot be calculated in the same fashion as done for the cebus and howling monkey study groups. To calculate a minimum home range size for the community, the number of grid cells that were

used by all of the identifiable spider monkeys, or which they had to pass through, were summed. Considering home range in this fashion, the spider monkey community used an area of 1.47 km^2 (Figure 4). The spider monkeys that were well habituated to the presence of an observer were primarily studied in one section of forest which was separated from a second block of forest by a narrow corridor. The second block of forest was rarely used by identifiable spider monkeys, and I believe that the spider monkeys using this area belong to a second community. If interspecific home range overlap is calculated within the section of forest in which spider monkeys were primarily studied, 95% of the area used by the cebus monkey study group and 96% of the area used by the howling monkey group were also used by identifiable spider monkeys.

Scan samples indicated that during 15.4% of the observation time, another primate species was within 50 m of the primate species being observed. Again, this value is probably an underestimate, since it is often difficult to observe primates that are 50 m away, especially if they are silent and inactive. On 177 occasions, two or three of the primate species were in the same tree at the same time. Fourteen of these occasions resulted in one of the primates displacing the other from the tree. Spider monkeys dominated both cebus and howling monkeys (spider displaced howler on 9 occasions, and cebus on 3). While cebus monkeys appear dominant to howlers, ony on one occasion did they displace a group from a tree, Once displaced by spiders, cebus monkeys always moved out of the area, whereas the howlers would often wait in the vicinity until the spider monkeys had fed and left the tree, then returned to eat what food remained. Since spider monkeys were shown to functionally deplete the trees they used (Chapter 3), it seems likely that howling monkeys were less able to acquire food items after being displaced than if they were able to feed in the tree unmolested. In addition, by being displaced howlers were probably forced to take food items of lower quality (e.g. less ripe fruit) than they would have if they were not displaced by spider monkeys.

For a number of tree species this type of interaction likely altered the dietary choices of the primates. In particular, for a number of fruiting trees such as Swartzia cubensis and Ficus sp. that occurred at low density, it was possible for one primate species to monopolize

the resource. Once spider monkeys located such a food source, they often excluded howlers from it for the major part of the day. On a number of occasions howlers were seen foraging in the vicinity of a fruiting fig tree that was being used by spider monkeys, only entering it once the spider monkeys had left the area late in the afternoon.

Contemporary theory on resource partitioning suggests that coexisting species should differ in their diet in order to minimize competition. Dietary overlap has been logically used in two opposing fashions; first, high dietary overlap has been used to suggest that intense selective pressure is currently causing diets to diets (Wiens and Rotenberry 1979), and secondly, low dietary overlap demonstrates that intense selection for dietary divergence has occurred in the past (Connell 1980, Holmes and Pitelka 1968, Wiens 1977). Thus, to examine the effects of dietary overlap on the nature of the pimates diets, both periods of high and low overlap must be examined. For each species pair all months were ranked by dietary overlap and the top quarter was arbitrarily chosen to represent the conditions experienced when dietary overlap was high, and the bottom quarter was chosen to represent conditions of low overlap. Of the 18 months selected in this fashion only 3 were the same month in the different years. Thus, there was little consistency between years in terms of which months had either high or low dietary overlap. At the time of high dietary overlap, the monkeys were primarily eating fruit; however, there were also instances involving high overlap for flowers and leaf buds. The trees for which a high level of overlap occurred varied from being common (34.4 individuals/hectare) to rare (0.50 individuals/hectare). Some of these plant species were preferred foods, while others were not (selectivity ranged from 0.04-31.7). Some of the species for which overlap was high bore food items for a short period ($>$ 1 month), while others bore food items for extended periods (maximum 12 months). Similarly, when dietary overlap was low, there was little consistency in the types of foods being used by any of the three primate species. For instance, during the months of the lowest dietary overlap for spider and cebus monkeys, spiders fed primarily on leaves in one month, on a combination of flowers and fruit in the next month, and primarily on fruit in the third month, while the cebus monkeys fed primarily on fruit (of different species) and insects in all months. Since

the climate of Santa Rosa is highly seasonal and many plants exhibit similar phenological cycles, one might expect there to be synchronization in dietary overlap between the species pairs. Nno consistent period of either high or low overlap existed for all species pairs, and there was no temporal sychronization in the degrees of dietary overlap (Kendals test of concordance $W=0.314$, $P>0.05$).

Discussion

While the major emphasis in primate ecology has been to identify consistent patterns, not to examine variability, a large body of evidence suggests that variability, such as was found here, commonly occurs in primates (Clutton-Brock 1977, Struhsaker 1975, Waser 1977). By simultaneously examining the diets of the three primate species found in Santa Rosa, it was possible to quantify the extent of the variability in diet and its influence on interspecific dietary overlap. The diets of all three species varied considerably on a monthly and annual basis. Variability occurred both in terms of the types of foods consumed (fruit vs leaves, etc.) and in what plant species were exploited. This variation in diet contributed to the variability in interspecific dietary overlap between the three primate species. There was little consistency between years in when dietary overlap was likely to be high or low, or in the types of trees that were the source of the overlap. A number of other studies on a variety of animal species have demonstrated great variability in diet similar to the results obtained in this study (Feinsinger 1976, Gautier-Hion 1980, MacKinnon and MacKinnon 1978, 1980, Wiens 1977, Wiens and Rotenberry 1979, Rotenberry 1980).

If primates commonly have flexible diets, this will influence how they interact with other species in their community. The view that primate communities exist in balanced coexistence, where each species exploits a different combination of resources, has been shaped by studies which have not examined variability and its consequences. Variability in diet will influence the relative importance of dietary overlap as a selective pressure favoring the divergence of diets. For the species studied here, high variability in diet, overlap, and in the plants over which overlap occurs, are likely to result in dietary overlap only acting as a

selective pressure determining diet choice on a intermittent basis (Strong 1983, Wiens 1977). In fact, overlap may only be a significant force on a supra-annual basis, possibly being associated with periods of atypical conditions (e.g. fruit crop failure, Foster 1982, or cyclone destruction, Dittus 1985). If these periods of "significant" overlap occurred on a periodic basis which was much greater than the study species' generation time, or if the strategy which was most profitably used during these periods varied, the predictability of success of a given genotype is likely to be low. Thus, heritability of a specific diet favored by dietary overlap will also be low. For primates, it seems probable that the profitability of a specific diet will vary between periods of "significant" overlap. Not only do primates have diverse diets, and thus many options as to which types of foods to eat during any period, but also the diet in different regions, between which gene flow is possible, will likely differ. The particular conditions favoring dietary divergence is likely to be site dependent. Given the level of variability shown between neighboring groups or populations in other studies (cited above), the diets used to deal with the periods of "significant" overlap will probably vary between sites.

Another factor that likely decreases the importance of competitive interactions in determining diet, concerns the fact that each species of monkey is not responding just to the pressures exerted on it by other primates, but to all of the species with which it overlaps in diet. In tropical communities many species often feed on the same food resource. For example, Beebe (1916) observed 51 tropical bird species entering a single fruit tree, and Willis (1966) lists 28 species of birds using the berries of one species of small tree. Rockwood and Glander (1979) documented an example of dietary overlap between two phylogenetically unrelated species when they observed overlap between howling monkeys and leaf cutter ants (see also, Emmons 1980, Estrada and Coates-Estrada 1985, Estrada et al. 1984, Fleming 1979, Gautier et al. 1980, Glander 1979, Terborgh 1983). These arguments suggest that although behavioural interactions, such as the displacement from food trees do occur, it is unlikely that interactions occurring between just the primate species are strong forces determining their diets.

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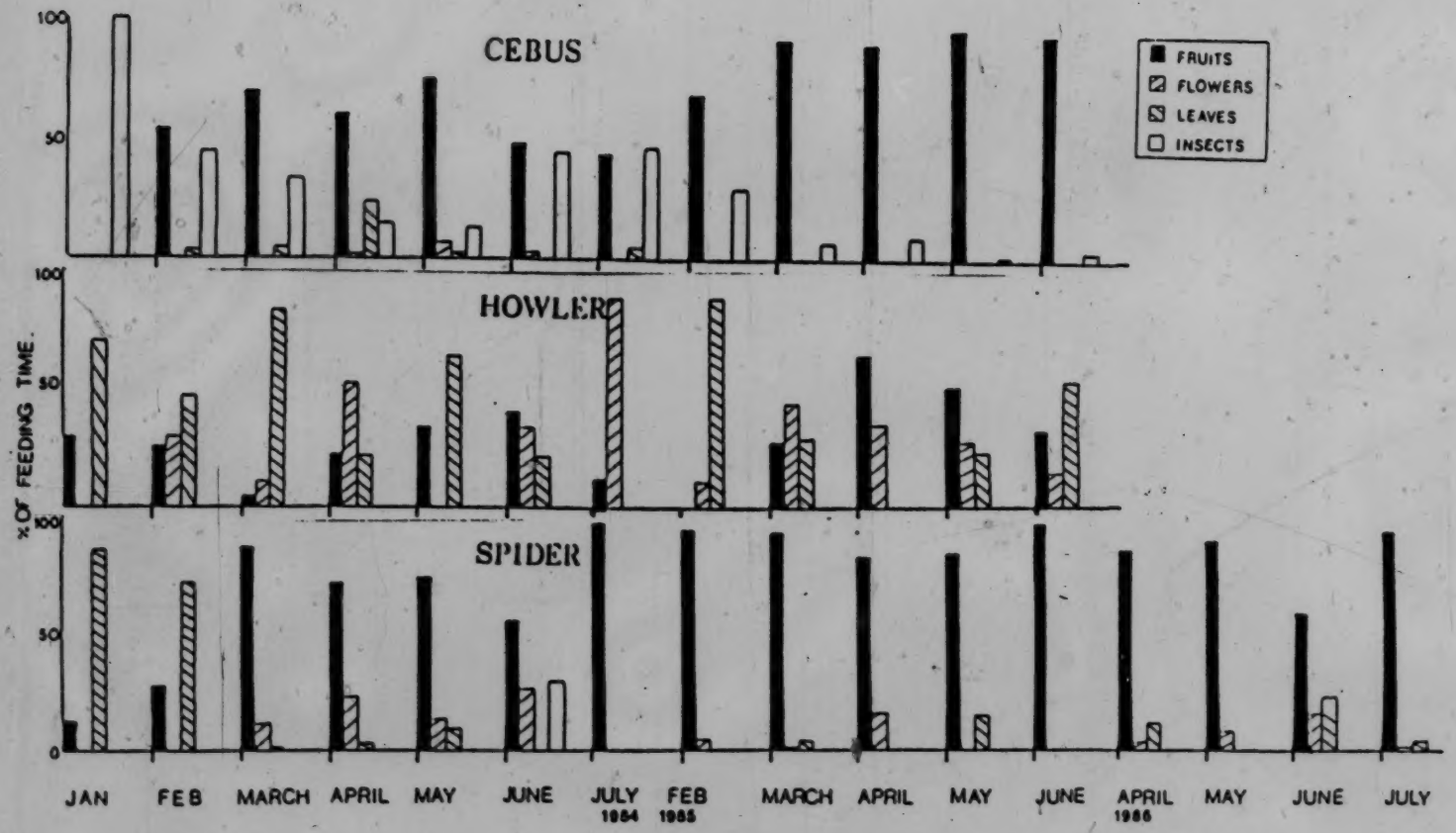

Figure 1.

The percentage of the observed feeding time that the three species of primates of Santa Rosa National Park, Costa Rica spent eating different type of foods in each month of the study.

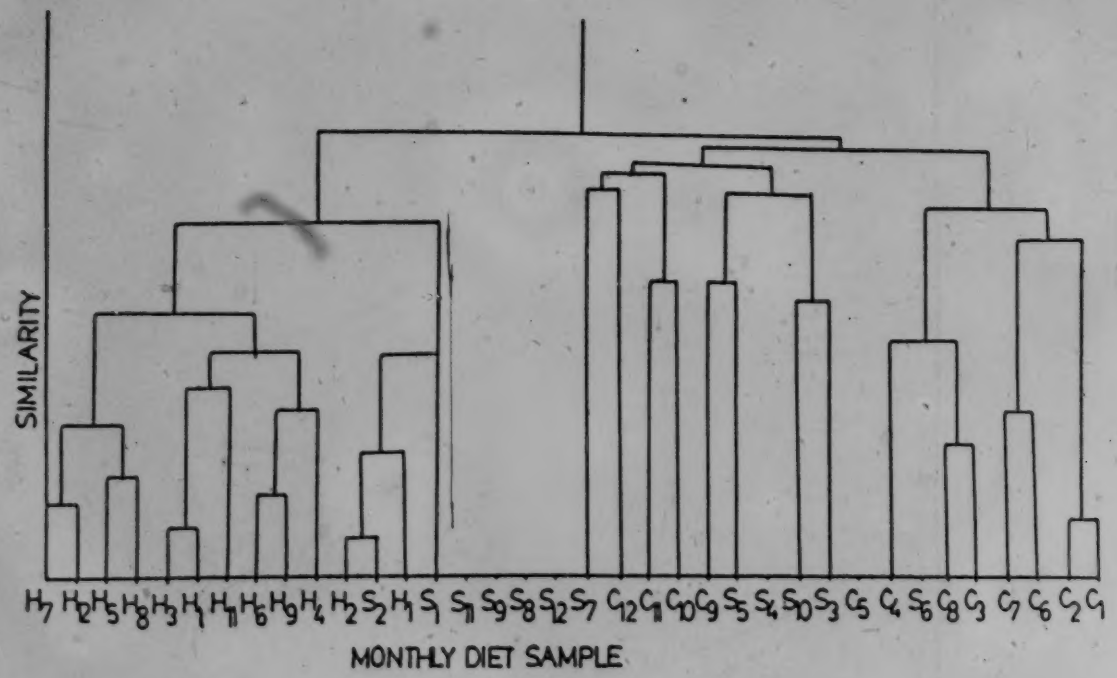
SIMILARITY
H7 H2 H5 H8 H3 H1 H11 H6 H9 H4 H2 S2 H1 S1 S11 S9 S8 S12 S7 C12 C11 C10 C9 S5 S4 S10 S3 C5 C4 S6 C8 C3 C7 C6 C2 C1
MONTHLY DIET SAMPLE

Figure 2.

A clustergram depicting the similarity in the diets of the three species of primates in Santa Rosa National Park, Costa Rica. The unit of comparison was the types of foods eaten (i.e. fruit, flowers, leaves, insects). For the monthly dietary sample, C represents Cebus capucinus, S represents the spider monkey, Ateles geoffroyi, and H represents the howling monkey, Alouatta palliata. The numbers in the monthly diet sample represent the consecutive months of the study, i.e. 1=January 1984, 2=February 1984, 3=March 1984, 4=April 1984, 5=May 1984, 6=June 1984, 7=July 1984, 8=February 1985, 9=March 1985, 10=April 1985, 11=May 1985, 12=June 1985.

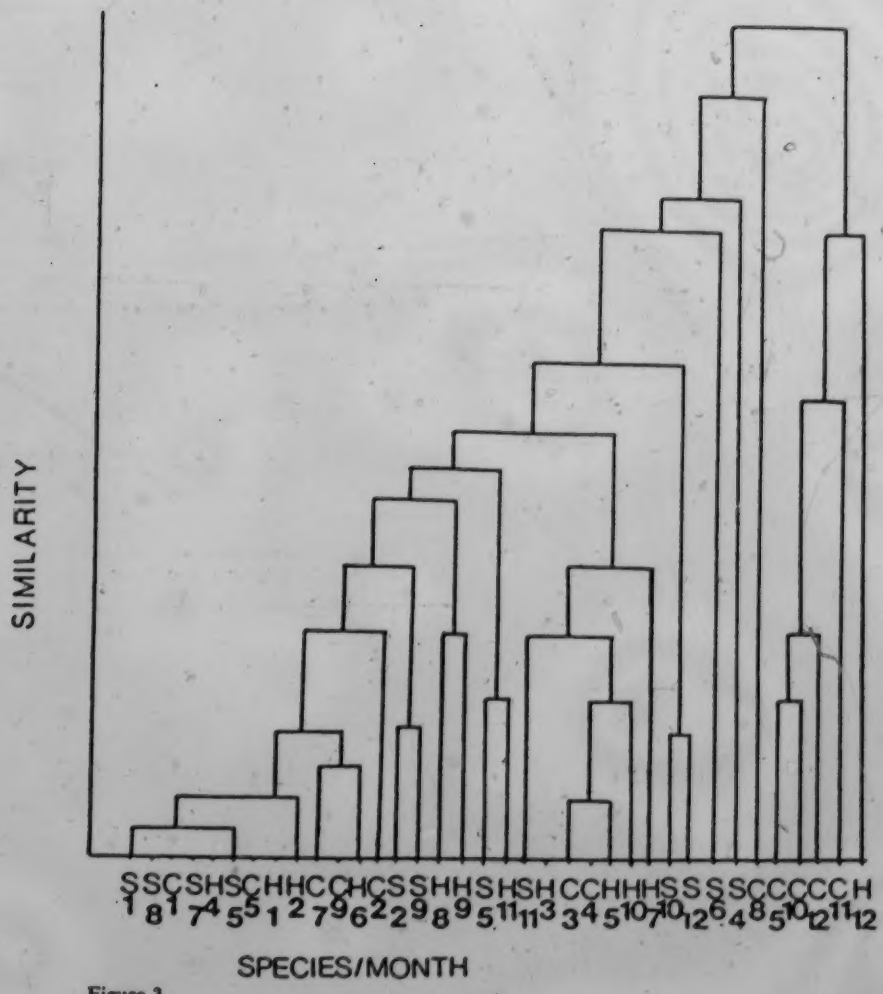
SIMILARITY
SSCSHSCHHCCHCSSHHSHSHCCHHHSSSSCCCCCH
1 8 1 7 4 5 5 1 2 7 9 6 2 2 9 8 9 5 11 11 3 3 4 5 10 7 10 12 6 4 8 5 10 12 11 12
SPECIES/MONTH

Figure 3.

A clustergram depicting the similarity in the diets of the three species of primates in Santa Rosa National Park, Costa Rica. The unit of comparison was the six most commonly eaten food items (i.e. species, part) consumed by each primate species. For the monthly dietary sample, C represents Cebus capucinus, S represents the spider monkey, Ateles geoffroyi, and H represents the howling monkey, Alouatta palliata. The numbers in the monthly diet sample represent the consecutive months of the study, i.e. 1=January 1984, 2=February 1984, 3=March 1984, 4=April 1984, 5=May 1984, 6=June 1984, 7=July 1984, 8=February 1985, 9=March 1985, 10=April 1985, 11=May 1985, 12=June 1985.

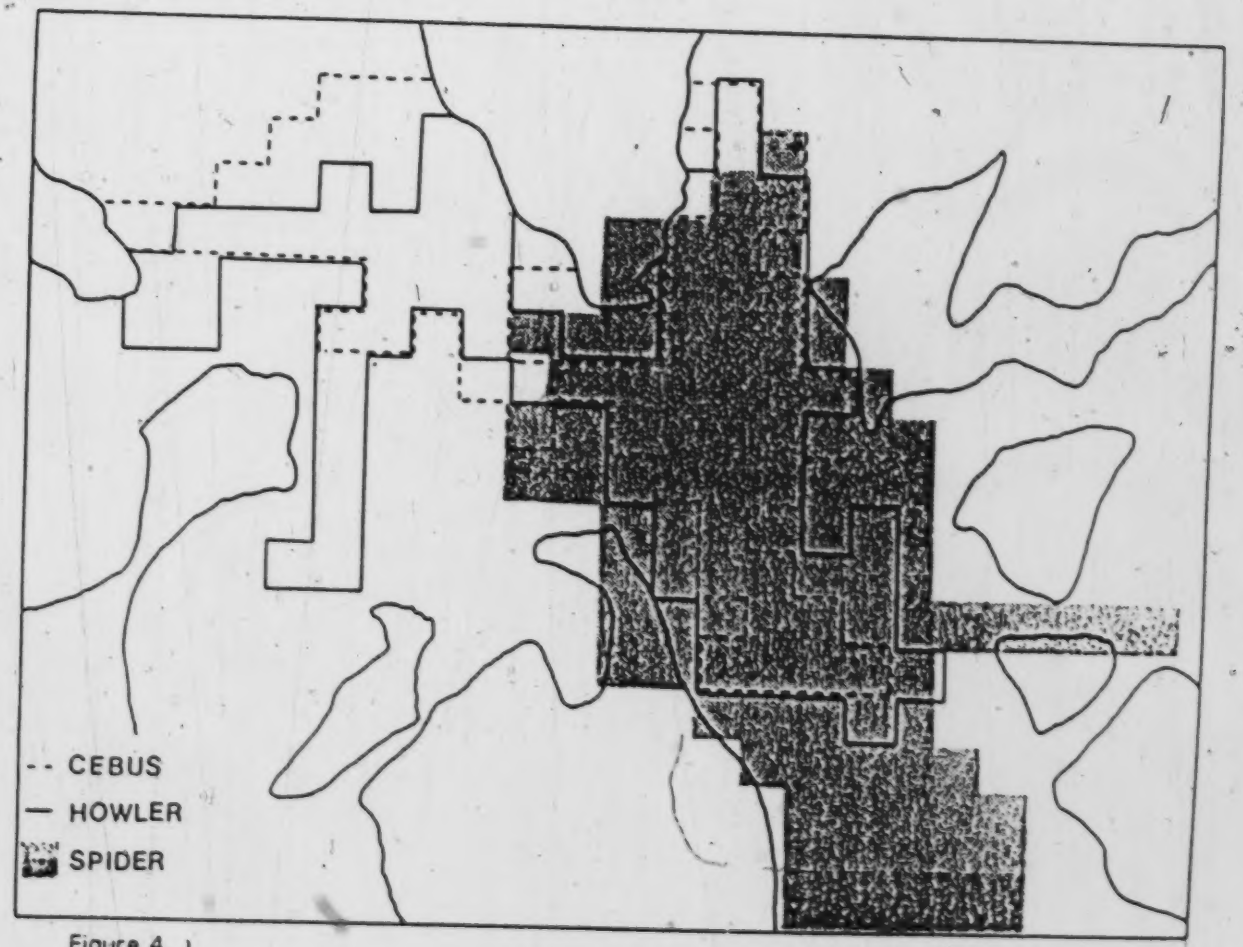

Figure 4.

The area of home range overlap for the three species of primates found in Santa Rosa National Park, Costa Rica.

Table 1.

Percentage of total feeding time spent eating different types of foods by the three species of primates found in Santa Rosa National Park, Costa Rica. The data are derived from focal animal observations (*Cebus capucinus* 171 hours; spiders, *Ateles geoffroyi* 335 hours; and howlers, *Alouatta palliata* 393 hours).

Plant Part		Cebus	Howler	Spider
Fruit		81.2	28.5	77.7
Flower		0.2	22.5	9.8
Leaves	Mature	0.5	27.7	1.2
	Young	0.7	17.4	7.3
	Buds	0.1	3.9	2.6
Insects		16.9	0.0	1.3

Table 2.

A description of the pattern of feeding of the three species of primates living in Santa Rosa National Park depicting those plant parts which were used for more than greater than 1% of the feeding time.

Plant	Spiders			Howler			Cebus		
	%of total feeding time	range	CV	%of total feeding time	range	CV	%of total feeding time	range	CV
Ficus sp. fruit	29.2	7-72	85	15.5	2-40	163	2.0	1-30	232
Muntingia calabura fruit	16.1	0-45	169	---	----	---	17.8	7-31	83
Mastichodendron capiri fruit	6.6	2-42	147	3.1	0-30	259	---	----	---
Dipterodendron costaricensis fruit	6.3	8-41	216	---	----	---	---	----	---
Pithecellobium saman flowers	2.9	0-4	196	6.8	0-52	228	---	----	---
Tabebuia ochracea flowers	2.8	0-8	235	---	----	---	---	----	---
Coccoloba venosa fruit	2.7	0-3	209	---	----	---	---	----	---
Brosimum alicastrum fruit	2.7	0-15	203	5.5	2-37	331	---	----	---
Bursera simaruba fruit	2.4	0-22	270	2.4	0-16	214	---	----	---
Ficus sp. young leaves	2.4	0-16	370	5.1	0-62	348	2.4	0-21	354
Sloanea terniflora fruit	2.2	0-41	354	---	----	---	34.1	1-87	152
Manilkara chicle fruit	2.0	7-32	198	2.7	2-30	218	---	----	---
Hymenaea courbail leaf buds	2.0	1-88	288	2.8	2-70	277	---	----	---
Brosimum alicastrum mature leaves	---	----	---	10.2	4-40	188	---	----	---
Manilkara chicle flowers	---	----	---	7.4	0-33	214	---	----	---
Lonchocarpus costaricensis flowers	---	----	---	5.2	0-44	207	---	----	---
Ficus sp. leaf buds	---	----	---	2.0	0-22	219	---	----	---
Bursera simaruba mature leaves	---	----	---	3.8	0-39	225	---	----	---
Bursera simaruba flowers	---	----	---	2.7	0-14	355	---	----	---
Castilla elastica leaf buds	---	----	---	2.4	0-11	193	---	----	---
Brosimum alicastrum leaf buds	---	----	---	2.3	0-16	214	---	----	---
Brosimum alicastrum young leaves	---	----	---	2.2	0-14	235	---	----	---
Luehea speciosa fruit	---	----	---	---	----	---	4.4	0-56	286
Quercus oleoides fruit	---	----	---	---	----	---	3.5	0-32	213
Sciadodendron excelsum fruit	---	----	---	---	----	---	2.5	0.28	312

Table 3.

Intraspecific dietary overlap between adjacent months for the primates of Santa Rosa National Park, Costa Rica.

	Month	Cebus	Howler	Spider[1]
1984	Jan/Feb	0.0	40.3	46.2
	Feb/March	36.3	26.7	31.5
	March/April	48.6	6.5	28.5
	April/May	32.3	9.1	45.3
	May/June	21.2	5.9	48.9
	June/July	51.9	2.3	45.3
1985	Feb/March	19.6	23.3	40.1
	March/April	36.7	0.0	44.2
	April/May	45.7	45.1	34.9
	May/June	61.9	41.1	19.4
	Average	35.4	20.0	38.4

Table 4.

Intraspecific dietary overlap between the same months in two different years (1984 and 1985) for the three species of primates found in Santa Rosa National Park, Costa Rica.

Month	Cebus	Howler	Spider
Feb	42.9	21.5	20.0
March	46.6	18.5	28.9
April	51.9	44.4	49.3
May	62.3	37.1	53.7
June	9.2	20.9	27.5
Average	42.6	28.5	31.9

Table 5.

Interspecific dietary overlap per month for the three species of primates in Santa Rosa National Park, Costa Rica.

	Month	Howler/Spider	Cebus/Spider	Cebus/Howler
1984	January	83.7	0.0	0.0
	February	30.3	0.0	0.0
	March	0.0	34.9	0.2
	April	13.1	43.0	30.1
	May	29.1	21.5	19.0
	June	31.9	36.0	7.0
	July	0.7	38.0	0.0
1985	February	0.0	12.4	0.0
	March	0.0	29.1	0.0
	April	39.4	12.4	3.2
	May	25.8	13.5	0.0
	June	20.7	42.5	0.0
	Average	22.9	23.6	5.0

V. Ecological Constraints on Group Size in Three Species of Neotropical Primates

Introduction

Recently several attempts have been made to formulate principles which govern animal group size and to predict how animals are distributed in space. Resource availability can influence optimal group size either by limiting the number of animals an area can support or, if the costs and benefits of obtaining the resources are a function of group size, by influencing foraging efficiency. Density and distribution of food resources are the most notable resource variables suggested to limit group size (S. Altmann 1974, Bradbury and Vehrencamp 1976a,b, Caraco et al. 1980, Caraco and Wolf 1975, Crook 1965, 1970, 1972, Eisenberg et al. 1972, Horn 1968, Jarman 1974, Klein and Klein 1975, 1977, Kummer 1971, Leighton 1982, Leighton and Leighton 1982, MacDonald 1979, 1983, Terborgh 1983, Ward and Zahavi 1973, Wrangham 1979, 1980).

It is easy to understand how food abundance might influence the density of primates (Gaulin et al. 1980, Van Schaik 1983), but it is less apparent how variables such as the abundance, density, and distribution of resources might limit the size of individual groups. Animals must forage over an area that can adequately meet their energetic and nutritional requirements. It follows that an increase in group size will increase the area that must be travelled to find adequate food supplies (food abundance remaining constant). Thus, over a specific period of time individuals in a group that foraged in an area that met the needs of all group members would have travelled further and spent more energy than would be the case if they had foraged in smaller groups or alone (Milton and May 1976). With an increase in the time spent travelling, some point will be reached at which energy spent in travel exceeds the energy obtained from the environment, and a smaller group size should become advantageous. In this fashion ecological factors can influence movement patterns and thus foraging efficiency, and thereby set biological limits on the size of the groups that can efficiently exploit the food resources. Three aspects of a limiting resource can affect movement patterns

: (1) patch size; (2) the density of patches; and (3) the spatial distribution of the patches.

The physical size of a patch can limit the number of animals capable of using it at the same time, regardless of the amount of food in it. For example, Klein and Klein (1975) observed that when spider monkeys (Ateles belzebuth) fed on palm fruit they did so as solitary animals for there was only one perch available providing access to a cluster of fruit. The size of a patch also determines the abundance of food items and thereby influences the profitability of remaining in a patch (Estabrook and Dunham 1976). The abundance of food items available in a patch is not static, but changes as new food becomes available or as animals deplete the food items. The rate at which a patch is depleted will depend on a number of factors: the abundance of food items in the patch, the rate with which they are replenished, the number of animals using the patch, and the rate with which consumers exploit food items. With respect to the latter 2 factors, Ghiglieri (1984) described how the number of chimpanzees using a patch can influence the abundance of food items in a patch. He suggested that a patch containing enough food to support three chimpanzees for an hour, would support a group of 30 chimpanzees for only 6 minutes. Many experimental studies have demonstrated the importance of patch size on selection of feeding sites and travel time (for reviews see Krebs 1978, 1979, Pyke et al. 1977, Schoener 1971). In general, these studies suggest that animals tend to select large patches and attempt to minimize their travel time (see Chapter 3 for support of these suppositions for spider and howling monkeys).

The density of food patches can influence feeding efficiency by affecting inter-patch travel costs (when patches are depleted through use). When patches occur at high density, animals do not have to travel far to find adequate food resources; when patches occur at low density, animals must travel further to fulfill energy requirements. The distribution of patches can similarly affect the distance animals must travel once they leave a patch that they have depleted.

Following this line of reasoning, patches that are rapidly depleted, or patch characteristics (density and distribution) that incur high travel costs should favour small groups. Thus, when patches are small (they are depleted rapidly), at low density and clumped

(animals must move between clumps and thus a large amount of energy must be spent travelling between food patches), a large group will by necessity have to visit many areas; however, if group size is reduced, patches will support animals for longer periods and travel can be minimized. Following this logic, I hypothesize that the largest groups should be found when patches are large, uniformly distributed, and at high density and the smallest groups should be found when patches are small, clumped and occur at low density. Intermediate levels of size, density, and distribution of resources should correspond to intermediate group sizes. In contrast, if patches are clumped but the food in them is abundant enough that animals need not move between clumps or if patches are non-depleting, a clumped distribution of patches can result in little need to travel and thus large groups can form (e.g. MacDonald 1979).

The objective of this study was to examine the hypothesis that subgroup size is a function of the size, density, and distribution of food patches for the three species of primates in Santa Rosa National Park, Costa Rica (Ateles geoffroyi, Cebus capucinus, Alouatta palliata). I assume selective pressures exist that favour group living in these primate species and only examine factors that limit group size, rather than factors that favour the evolution of group living.

Prior to analysing if food resources set limits on group size for these primate species, it is necessary to define a number of terms. A "group" is considered here as the largest stable social unit in which all members generally interact in an affiliative fashion and agonistic behaviour is infrequent, even when individuals that have been separated for some time reunite. A "subgroup" is any number of animals, less than the total for the group, that are associating together, taking part in coordinated activities, and maintaining relatively close spatial contact. A "patch" is an aggregation of food items that represent an area of high food density, the limits of which are defined by adjacent areas of low food density (Addicott et al. in prep., S. Altmann 1974, Hassell and Southwood 1978). To an animal, a food patch is perceived as an area structured such that it can use the area without interrupting its feeding activity (S. Altmann 1974).

The primates of Santa Rosa National Park offer an excellent opportunity to examine ecological determinants of group size. First, not only do the three species differ in social organization, but also the pattern of association within each species varies over time. Variability in association pattern is valuable, since an attempt can be made to relate subgroup size to environmental conditions and examine general models of group size. Secondly, a major food resource of all three species is fruit. Fruit occurs in relatively discrete locations and can be classified easily as available or unavailable, since most fruit changes its color or outward morphology in association with ripening (Janson 1983). These characteristics allow the density and distribution of major food resources to be clearly defined, something not possible in many previous socio-ecological studies (Crook 1965, 1972, Clutton-Brock 1974, 1975, Emlen and Oring 1977). Such lack of clear definition has limited the development of theory explaining group size (Addicott et al. in prep.). Finally, groups of each species of primates in Santa Rosa National Park are habituated to observation, facilitating an assessment of relationships between behaviour and ecological conditions.

Methods

Study Site and Study Groups

The study was carried out in Santa Rosa National Park, Costa Rica during four field seasons encompassing 24 months (July and August 1983, January to August 1984, January to July 1985, and February to August 1986). During the last year of the project, spider monkeys were the focus of the investigation. Details of the study site, climate, vegetation, and behavioural sampling methods were presented in Chapter 2.

A group of each of the three species, whose home ranges overlapped extensively, were chosen as study subjects. The howling monkey group had on average 40 individuals. Howling monkeys have typically been described as living in relatively stable, cohesive, multimale-multifemale social groups (Carpenter 1965, Chivers 1969, Estrada 1984, Gaulin et al. 1980, Gaulin and Gaulin 1982, Glander 1980, Milton 1980, Smith 1977). The study group had a multimale-multifemale type of social structure, but the group was neither stable nor

cohesive. The group frequently fragmented into subgroups which were spatially separated for periods that lasted up to 4 weeks. The howling monkeys were in subgroups, rather than a single group, for 84% of the total observation time. The group tended to split into two approximately equally sized subgroups. Occasionally, one of these subgroups would also fission (mean subgroup size = 19.3 individuals, n = 324 sightings). The composition of the subgroups changed frequently as animals moved between them. Adult males were the most mobile age/sex class; recognizable males were often seen moving between subgroups as solitary animals (solitary animals when moving between subgroups were not considered in the calculation of mean subgroup size). When subgroups united, agonistic behaviours were rarely observed. Similar fragmentation of howling monkey social groups have been observed on Barro Colorado Island, Panama (K. Milton personal comm.).

The cebus monkey group contained on average 26 individuals. This was a large group for Santa Rosa; the mean cebus group size for the park was 14.6 individuals (Fedigan et al. 1985). The group always maintained a multimale-multifemale type of social organization similar to that described elsewhere (Buckley 1983, Defler 1979, Janson 1984, 1985, Oppenheimer 1968, Robinson 1981, 1986, Terborgh 1983) and was never observed to fragment into subgroups. However, spatial cohesion between members varied over time.

Spider monkey social organization is poorly understood. Spiders are typically described as living in multimale-multifemale social groups. These groups consist of amicably interacting individuals which rarely come together to form a cohesive unit, but tend to be found in small subgroups of 3 to 5 individuals which have unstable composition (Carpenter 1935, Fedigan and Baxter 1984, Izawa et al. 1979, Klein 1971, 1972, Klein and Klein 1973, 1975, 1977). An estimate of the minimum size of the spider monkey community was obtained by summing the maximum counts of all age/sex classes seen in one year. Using this method the community was estimated to contain 42 individuals; 4 adult males, 17 adult females, 2 large immature males, 4 large immature females, 7 small immatures, and 8 infants.

Behavioural Observations

Behavioural data were collected using a focal animal sampling regime to obtain a record of not only what the subject did, but also of what was done to the subject (J. Altmann 1974). Using this sampling procedure, 394 hours of focal animal data were collected on howling monkeys, 335 hours on spiders, and 171 hours on cebus monkeys. Normally the species chosen to be sampled was alternated each day, although this depended somewhat on the ease with which each species could be located on a particular day. The length of the focal animal session was set at 10 minutes. If the subject was lost prior to the end of the session, the session was terminated and the data discarded. When possible, the animal to be sampled was chosen based on a fixed rotation between age/sex classes. Half way through the focal animal session, a measure of the relative spatial cohesion of the group was obtained by estimating the number of animals within 10 meters of the subject (the "Index of Spatial Cohesion"). The 10 meter cut off level was chosen because it was felt that all animals within this distance could be seen, irrespective of the type of forest the animals were using (see Chapman et al. in prep.). An attempt was made to obtain a complete record of each species' activity during a 3-week sample period so that at the end of this period an equal number of observations were made in each hour of the day. The location of the group being followed was recorded every 10 minutes as a coordinate of a 120 m by 120 m grid superimposed on an aerial photograph. The error in estimating location was likely small, and rarely resulted in the group being recorded in the wrong cell of the grid.

When viewing conditions were ideal and every item handled by a feeding animal could be seen and counted, the fate of each food item (i.e., eaten, partially eaten, dropped, etc.) was recorded in relation to the time since the patch was first entered by the subgroup. This information was collected to determine if the rate of food intake decreased with the time spent in the patch.

Ecological Sampling

Three ecological variables were considered of particular interest in predicting subgroup size; the size, density, and distribution of food patches. To quantify these variables, the most commonly used food plant species were identified for each primate species from the preceding

3 weeks of behavioural observation, and the location and phenological status of all adult trees of these species were determined in three 4-hectare grids. Normally only four plant species were chosen to represent the ecological conditions for a 3-week period. The use of only these few "major" plant species was justified since they always accounted for over 91% of all of the time spent feeding. An adult tree was considered as any individual that had attained a diameter at breast height (DBH) greater than or equal to that of the smallest individual seen to bear fruit. The grids consisted of 400 cells each 10 m by 10 m in size. Corners of the cells were marked with individually labelled steel posts. The phenological information recorded involved assessing the stage of leaf development (no leaves, leaf buds, young leaves, mature leaves) and noting the presence or absence of fruit and flowers. In 1984, phenological data were recorded on the plant species that the preceding 3 weeks of behavioural sampling had demonstrated to be important. In 1985 and 1986, the phenological status of all individuals of the major plant species used by the primates any time during the study were determined. After January 1985, when a plant species was used that had not been eaten in the past, phenological data were recorded on it in all subsequent ecological sampling periods. The length of the sampling period was chosen because in a 3-week period an adequate behavioural sample of each of the primate species could be obtained and because the phenological cycles of the majority of the plants used were measurable using this time scale. The majority of the food plants used by the monkeys bore food items for more than three consecutive weeks; thus individual trees possessing food items at the beginning of the sample period still possessed them at the end of the period. Individuals of the few species of plants that were exceptions to this (e.g. flowering Tabebuia ochracea) could be identified by looking for food items that had fallen to the ground. Ideally, the size of a food patch would be represented as the number of food items in the patch; however, because the large number of patches used by the monkeys prohibited the actual counting of food items, patch size was represented as DBH. For several tropical tree species, DBH has been shown to accurately reflect the reproductive capacity of fruiting individuals (Leighton 1982, Leighton and Leighton 1982, McDiarmid et al. 1977, Peters et al. in prep., Janzen personal comm.).

To analyse the relationship between patch characteristics and subgroup size, only those trees of a size that can be used by the monkeys were included in the calculation of density and distribution of food resources. Howlers rarely used small adult food trees (<20 cm DBH), whereas cebus and spider monkeys frequently fed in such trees. This interspecific difference is probably related to differences in body size and locomotory patterns between the three species (Cant 1986). Howlers fed in large food trees (>20 cm DBH) more often than would be expected based on the size of the food trees available ($X^2=115.8$, $P<0.001$, $n=88$ trees). Studies of howling monkeys on Barro Colorado Island also indicated selection for large trees (Smith 1977, Milton 1980). To decide the size of the tree to include in this analysis, a frequency distribution was made of the DBHs of all the trees that howlers were observed to use. From this distribution it was clear that howlers rarely (<5% of the observations) used trees with a DBH less than 20 cm. In contrast, trees that were less than 20 cm constituted 25.0% of the trees used by spider monkeys and 34.6% of those used by cebus monkeys. Thus, only trees with a DBH greater than 20 cm were used to calculate the density and distribution of food resources for howlers; for the other species all adult trees were used in the calculation.

To determine the distribution of the adult trees that were bearing food items, the "Coefficient of Dispersion" (CD) was calculated (Milton 1980, Pielou 1969, Sokal and Rohlf 1981, Southwood 1966). Since the aim of this analysis was to determine the distribution of food items, not the distribution of food trees, each food tree was weighted by its size (DBH), such that the value for a cell of the grid was the sum of the DBHs of all food trees. The value of the CD is greater than 1 when the distribution pattern is clumped, less than 1 if the pattern is uniform, and equal to 1 if the pattern is random. The density of food trees was calculated from counts of individual trees in the 3 grids and was represented as individuals per km^2. The density of food trees was weighted by tree size by multiplying the mean DBH of the food plant species by the number of trees in the grids and dividing the product by the area of the grid. One-tailed tests were used where the direction of the relationship being examined was predicted from the model. If no prediction was possible two-tailed tests were used.

Results and Discussion

Assumptions and Their Validity

The line of reasoning used to predict relative subgroup size has a number of assumptions which should be discussed and, in so far as possible, validated. First, I assume that these primate species use resources that can be considered to occur in patches. In Chapter 3 I have shown that the plant major food resources used by each of the primates in a 3-week sample period tended to occur at low density (mean # of patches/hectare 4.8 spiders, 8.0 howlers, 6.5 cebus). Often only a single individual of a preferred food species (e.g. Ficus sp.) occurred in the group's home range. Thus, the food resources used by these primates tended to be in discrete locations and far apart. In addition the average time spider monkeys spent moving from one food tree to another was 702 seconds (range 5 to 3660 seconds, based on 172 observed movements). Similarly, in the 90 observed movements by howlers, the group spent an average of 402 seconds moving between trees in which they fed (range 10 to 1421 seconds). In contrast movements within trees were of short duration. 94% of the movements of howlers within trees were less than 30 seconds and 97% of the spider monkey movements in food trees were less than 30 seconds. It seems reasonable to consider that the resources used by these primate species were found in discrete patches.

Secondly, for subgroup size to be a response to the proposed ecological conditions I assumed that as subgroup size increases, the area that must be searched to find food for all group members also increases. This assumption can be tested for spiders and howlers since observations were recorded for subgroups of different sizes (Figure 1,2). A positive correlation existed between subgroup size and the time spent travelling for both howlers ($r=0.483$, $P<0.001$) and spiders ($r=0.461$, $P=0.027$; comparisons made between the sample periods, spiders $n=18$, howlers $n=14$).

Third, I assumed that increased time spent travelling associated with membership in large subgroups is a significant cost. For both howlers and spiders the positive association of travel time with subgroup size corresponded with a significant positive relationship between subgroup size and the proportion of the total observation time spent feeding (howlers

r=0.491, P<0.001; spiders r=0.565, P=0.007). That suggests that to find sufficient food, individuals in large subgroups must travel further than those in small subgroups, and that the added travel cost is compensated for by an increase in the time spent feeding.

The assumption that the primates deplete the patches they use was investigated in Chapter 3 following four lines of evidence; 1) all species were commonly observed feeding in a number of individual trees of the same species in direct succession; 2) for most food plants the rate of intake of food items during a feeding bout was significantly higher at the start of the feeding bout than later (for some tree species the rate did not change over the duration of a bout of similar or longer length, suggesting that this relationship is not caused simply by satiation); 3) for howlers and spiders which had variable subgroup sizes, as subgroup size increased members spent more time travelling, suggesting that large subgroups deplete patches of equal size faster than smaller subgroups; and 4) for spiders and howlers the amount of time spent feeding was generally a function of the size of the patch and the number of animals using the patch.

The argument presented to predict relative subgroup size may still hold if the assumption of patch depletion is not valid. If a subgroup was feeding on a non-depleting resource in a tree large enough to support all individuals, they may leave the patch prior to its depletion to obtain a required nutrient mix. In that situation the density and distribution of resources would still influence travel time, and thus subgroup size, as would be the case if the patches were depleted. However, patch size would have no influence on travel time.

Intraspecific Comparisons of Ecology and Group Size

I propose that relative subgroup size can be predicted from the size, density, and distribution of food patches, such that subgroups will be smallest when resources are clumped and found at low densities, and larger when resources occur at high densities and are uniformly distributed. To test this prediction the average size of the subgroups observed during each 3-week sample period were compared to the ecological conditions measured at the end of these periods (for spiders n=18, howlers n=14, cebus n=14). The average spider monkey subgroup size was related to the density and distribution of food resources (log

transformation $R^2=0.544$, $P=0.047$). Partial correlations of subgroup size and patch density, controlling for resource distribution (log transformation $r=0.521$, $P=0.047$) and subgroup size and distribution controlling for density (log transformation $r=0.129$, $P=0.190$), suggest that the density of food resources had a stronger influence on subgroup size than distribution of patches.

Howling monkey subgroup size was a function of the density and distribution of their resources, but only weakly (log transformed $R^2=0.773$, $P=0.056$). A partial correlation on this set of variables illustrates that this relationship is primarily a function of the distribution of resources, rather than the density of resources (log transformed subgroup size by distribution controlling for density ($r=0.836$, $P=0.0410$; subgroup size by density controlling for distribution ($r=0.0665$, $P=0.233$).

The ecological conditions that corresponded to the sample period when the spider monkey community had the largest and smallest mean subgroup sizes are depicted in Figure 3. The corresponding situations experienced by the howling monkey group are represented in Figure 4. Notice that, as predicted, when resources were clumped and at low density both the spider and howling monkeys were found in the smallest subgroups, whereas when patches are relatively more uniformly distributed and at high density, they were in larger subgroups.

Unlike both the spider and howling monkeys, the cebus monkey group did not fragment throughout the study. However, the degree of spatial cohesion of the group did change. The 'index of spatial cohesion' averaged 0.73 over all sample periods and ranged between 0.61 and 0.91. This variability in cohesion was not however, related to the density and distribution of resources (log transformed $R^2=0.002$, $P=0.961$).

A number of previous studies have suggested that if group size exceeds the capacity of the food patches, or if the size of the patch is too small for all animals to feed simultaneously, levels of agonism are higher. Waser (1977) found increased aggression in small patches as the size of mangabey groups increased. Klein and Klein (1977) also noted an increase in aggression when spider monkeys fed in small trees and Chivers (1977) observed the same relationship with siamangs. Sussman and Richard (1974) found that lemurs were

aggressive when food occurred in limited areas and that aggression was not related to the abundance of food. Few agonistic interactions (41 episodes in 335 hours of focal animal observations) were seen among the spider monkeys of Santa Rosa. In apparent contradiction to these previously mentioned studies, there was no relationship between agonistic behaviour and the size of a tree, or the number of animals using the tree (multiple regression of agonism by patch size and subgroup size; $R^2=0.210$, $P=0.788$).

Interspecific Comparisions of Patch Characteristics and Group Size

It is difficult to make direct quantitative interspecific comparisons of patch characteristics and group size or social organization. The most critical factor limiting such comparisons is that the value of a patch will likely differ between species. Patch quality can be influenced by a variety of factors including, the ability of members of a species to travel, the size of trees they can use, their foraging strategy, their body size, and their digestive capabilities. If species being compared have different average weights, then the value of a particular patch will likely differ between the species solely because of the differences in their body sizes. Relative to a large-sized species, those with small body size will decrease the food in a patch more slowly, will become satiated sooner, and can fit more animals in the physical space of a patch. Since metabolic rate varies with 0.75 power of body weight (Kleiber 1961), a species that is twice the size of another, will require 68% more calories than the smaller species. This comparison is extremely simplified, for caloric needs would vary with factors in addition to body size, including activity levels, and digestive patterns. For the primates involved in this study, adults of the largest species are almost 3 times the weight of adults of smallest species (Glander et al. in prep.). Consequently, body weight is likely to be an important factor in understanding how each species perceives its environment (see Terborgh 1983).

While it is not possible to make direct quantitative comparisons between species, the traits of each species that may influence the relationships between patch characteristics and social structure can be examined.

Comparing the cebus and spider monkeys it is evident that while both spiders and cebus are heavily dependent on fruit, which is localized in discrete patches. However, cebus monkeys did not respond to changes in food resources by forming subgroups, while the spiders did so readily. Perhaps in part because cebus monkeys have the option, not used by spider monkeys, of foraging for insects. Insects are more uniformly distributed than the fruit trees that were used (Wolda 1978a,b, Janzen 1973, Buskirk and Buskirk 1976). Thus, when a patch is occupied by other animals in the group or has been depleted by their feeding, an individual cebus monkey can still take part in profitable foraging activities by hunting for insects. When patches occurred at low density and hence a patch was more likely to be occupied or depleted, cebus monkeys tended to spend more time eating insects ($r_s = -0.700$, $P < 0.05$, $n = 14$). Similarly, in sample periods when the cebus monkeys were using trees that were small in size, and could hold only a few individuals at any one time, they again tended to spend more time feeding on insects ($r_s = -0.463$, $P < 0.05$, $n = 14$ sample periods).

Differences in the relationship between food patch characteristics and subgroup size in the spider and howling monkeys may be attributed to the folivorous aspects of the howlers diet. Leaf resources tend to be less temporally and spatially restricted than fruit (Chapter 2). Howlers also have more types of food items in their diet than spider monkeys (Chapter 2). These attributes of the diet of howling monkeys may provide individuals with foraging options if a patch is full or had been depleted by other animals in the group.

The analyses presented above suggest that an increase in group size results in higher travel costs for the members of spider and howling monkey groups, but are inconclusive for cebus monkeys since they did not form subgroups. The results for spiders and howlers are like those of Van Schaik et al. (1983) who found that foraging and travelling times increased with group size in different groups of long-tailed macaques (Macaca fascicularis). Similarly, Stacey (1986), who studied three different sized groups of baboons (Papio cynocephalus) in Amboseli National Park, Kenya, found that members of the smaller group spent less time feeding than members of the largest group; however, mean foraging efficiency did not vary with group size.

The findings obtained from the study of the primates of Santa Rosa and data from the studies just mentioned, indicate that an increase in primate group size will lead to stronger competition for food resources among group members which must be compensated for by changes in the animals' time budgets. The increase in food competition with increasing group size is likely disadvantageous. Van Schaik et al. (1983) and Van Schaik and Van Noordwijk (1983) demonstrated that as group size increases, competition for food resources increases, and for a number of primate species there is a reduction in the rate at which females give birth. Based on this evidence, I suggest that the advantage to primates of living in groups is not related to feeding. The fact that the cebus monkeys of Santa Rosa did not form subgroups while the other two primate species did so frequently, provides an indication of an alternative advantage to group living. Cebus are are likely more susceptible to the predators of Santa Rosa than either spiders or howlers, since they are the smallest and most terrestrial of the three species. A strategy to reduce the risk of predation is to stay in a large group in which predators are more likely to be detected and where predator defence is more efficient in comparison to small groups (Chapman 1986). Thus, for cebus monkeys, group fission might be advantageous from the point of view of foraging efficiency, but the cost associated with group fission may likely exceed any benefits obtained. This suggests that to develop a model of optimal group size, both resource variables and susceptibility to predation must be considered.

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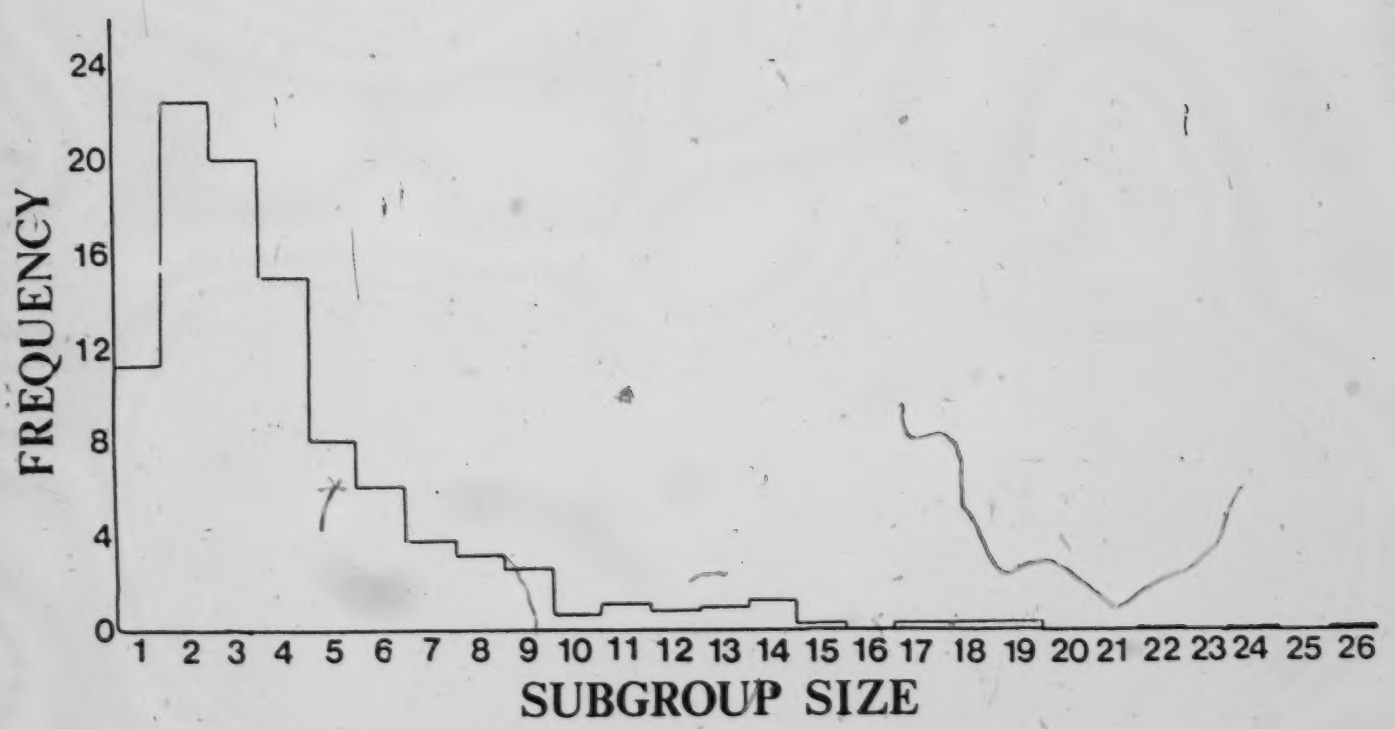


Figure 1.

Frequency histogram of size of the spider monkey (Ateles geoffroyi) subgroups seen in Santa Rosa National Park, Costa Rica.

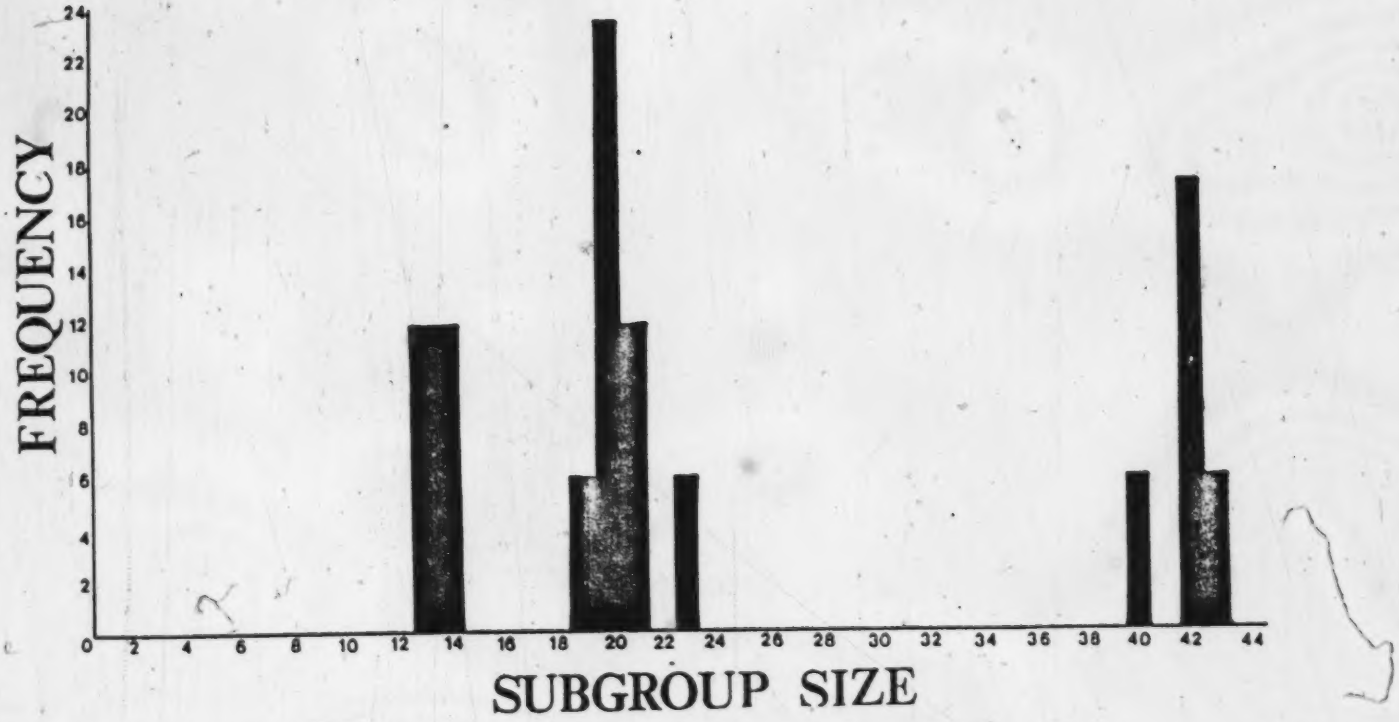


Figure 2.

Frequency histogram of the size of the howling monkey (Alouatta palliata) subgroups seen in Santa Rosa National Park, Costa Rica (does not include solitary individuals considered to be moving between subgroups).

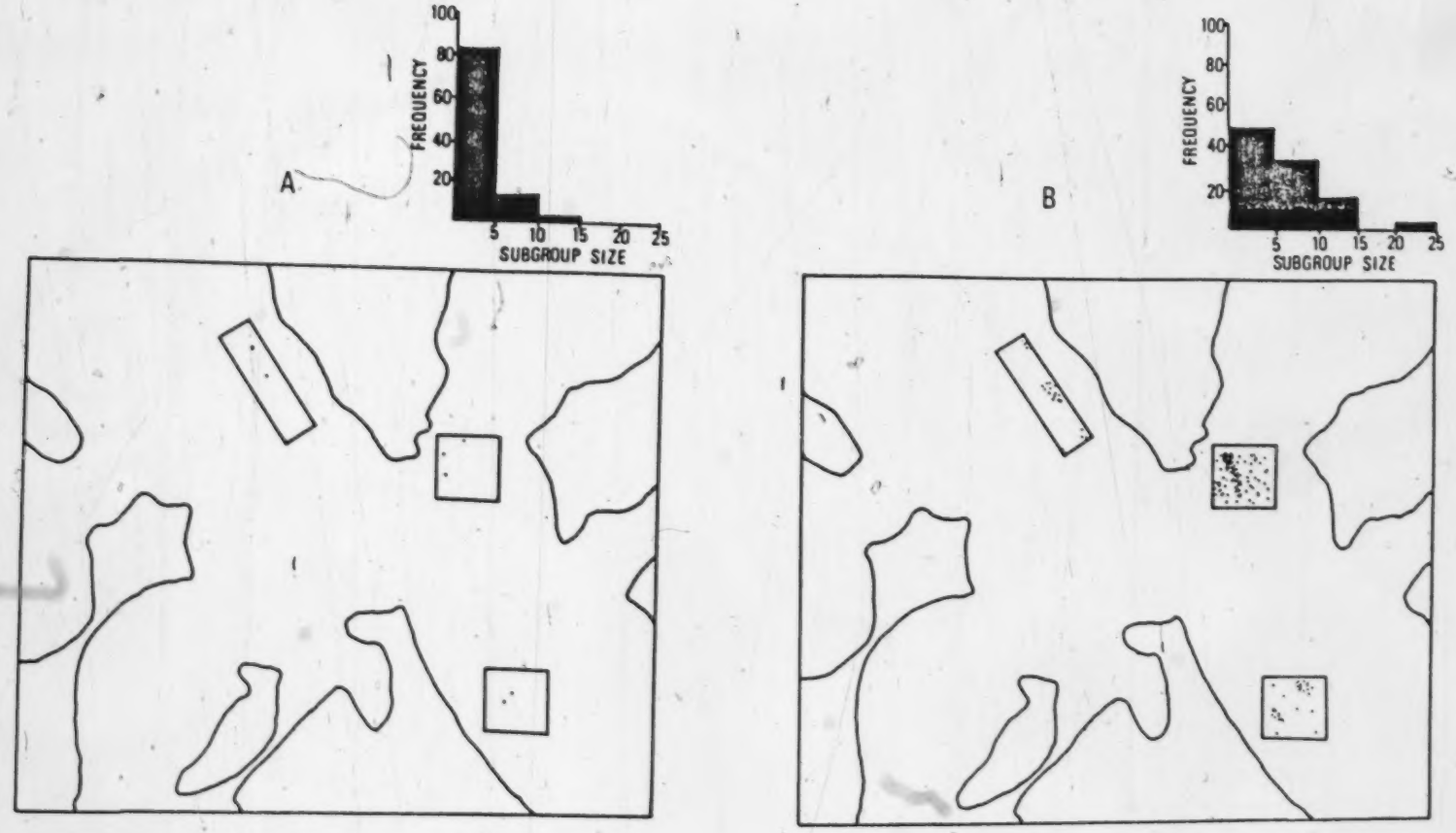


Figure 3
A. The ecological conditions that corresponded to the sample period when the spider monkey group was observed to occur in the smallest subgroups. The mean subgroup size was 2.3 individuals. Few trees were available, the density of food trees that were bearing food items was 50 individuals/ km^2 and they occurred in a clumped distribution (CD = 1.2). The mean DBH at this time was 50cm. B. The conditions when the largest subgroups occurred. The mean subgroup size was 6.4 individuals, food trees were found at high density (1543 individual/ km^2), and they were in clumps (CD = 1.1). The mean DBH at this time was 66 cm. A dot represents a tree regardless of size.

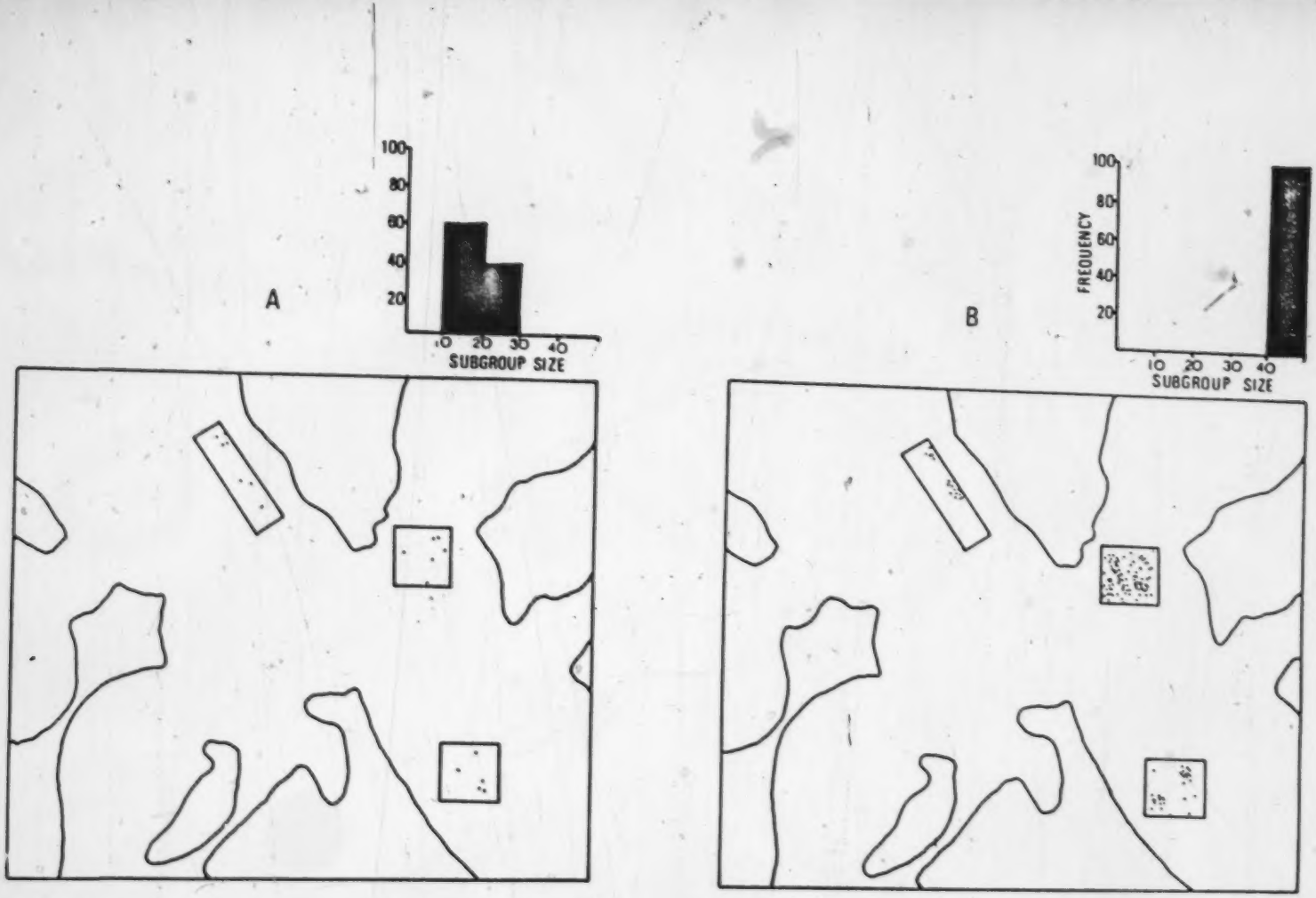


Figure 4
A. The ecological conditions that corresponded to the sample period when the howling monkey group was observed to occur in the smallest subgroups. The mean subgroup size was 13 individuals. Few trees were available, the density of food trees that were bearing food items was 158 individuals/ km^2 and they occurred in a clumped distribution (CD = 1.2). The mean DBH at this time was 51cm. B. The conditions when the largest subgroups occurred. The mean subgroup size was 40 individuals, food trees were found at high density (1408 individual/ km^2) and they occurred in clumps (CD = 1.1). The mean DBH at this time was 37.1 cm. A dot represents a tree regardless of size.

VI. General Discussion

The preceding chapters contribute to an understanding of the relationships between foraging strategies and determinants of group size in three species of neotropical primates. The thesis was developed by addressing four major objectives. First, in response to the general lack of suitable information needed to address specific behavioural ecological questions, chapter one provides a quantitative description of the foraging strategies and range use patterns of the three species of primates found in Santa Rosa National Park, Costa Rica (Ateles geoffroyi, Alouatta palliata, Cebus capucinus). As a focus for presenting this information, the chapter evaluates behavioural responses to changes in levels of food availability. Santa Rosa was an ideal location because it is a tropical dry forest situated in an area that experiences marked seasonal changes in rainfall. This extreme seasonality produced dramitic changes in the environmental conditions that the monkeys experienced.

From a conservation perspective, tropical dry forest is the most endangered of the once widespread habitats within Central America and a number of the species restricted to this habitat are in serious danger of extinction (including the spider monkey). Within Mesoamerica, dry forest once covered an area of 550,000 km^2. Today only 2.0% of this original forested area exists in a relatively undisturbed state and only 0.08% is presently protected in preserves (Janzen 1986). Thus, conducting research in such a dry forest habitat is of value simply because it creates both academic and local interest in the area.

In the second chapter, I demonstrated that the primates used resources that occurred in patches and depleted the patches through their use. Patch depletion is an assumption that underlies many behavioural ecological models, but has rarely been examined. The arguments proposed in Chapter 4 assume that the primates of Santa Rosa deplete the patches they use. An examination of which types of patches are depleted and the manner in which this depletion occurs, allows an assessment of the ecological factors underlying the different types of social organization in these species.

In the third chapter, an examination was made of the temporal variability in the dietary strategies of these three primate species with the objective of understanding how this variability might affect an animal's fitness and the probability of dietary overlap being an important selective pressure in the maintainance of dietary strategies. There was little similarity in what was eaten by any of the three species in one month and what was eaten by the same species in either the subsequent month, or in the same month in the subsequent years. The extent of this variability was such that a spider monkey's diet sampled over a month could share more in common with the diet of a howling monkey in that same month, than with the diet of spiders in the subsequent month or, in the same month in the next year. Dietary overlap between species changed considerably over time as a result of this high degree of variability, I proposed that the extent of this dietary variability should be considered when explanations of behavioural patterns are proposed based on observations made over a short period of time. For instance, interspecific dietary overlap is often suggested as a selective force influencing the diet of animal species. Yet, if dietary overlap was extremely variable and if the food items over which overlap occurred were likely to change, then the heritability of a specific type of diet favoured by interspecific competition for resources, would likely be low. Thus, a high degree of variability in dietary overlap would decrease the overall importance of competitive interactions in determining diet.

In the final chapter, information from the previous chapters was used to examine possible ecological constraints on the size of animal groups. The descriptive data from chapter 2 and the analysis of diets from chapter 4 were used to examine how well the relative size of the subgroups (or cohesion for cebus monkeys) of each of the three primate species could be predicted based upon the size, density, and distribution of each primate species' plant food resources. Central to the proposed argument is the assumption that primates use resources that can be considered to occur in patches that through their use are depleted; this assumption was validated in chapter 3. There is a good fit between the subgroup size predicted for spider and howling monkeys based on the size, density, and distribution of resources and the observed subgroup size (but not for the cohesion of the cebus monkeys). The significance of

this relationship lends strength to the proposed hypothesis that there are always pressures favouring animals to live in groups and that ecological conditions, in particular foraging costs associated with membership in large groups, constrain individuals to groups of particular sizes.

In addition, to developing a conceptual framework which is capable of predicting and understanding determinants of group size, I suggest that the form of social organization exhibited by the spider, and to a lesser extent the howling monkeys of Santa Rosa, in which animals form subgroups that are unstable in size and composition, has evolved as a response to rapidly changing resource conditions (Appendix 2).

References

Janzen, D.H. 1986. Guanacaste National Park: Tropical Ecological, and cultural restoration. Editorial Univ. Estatal a Distancia, San Jose, Costa Rica.

Appendix 1

This appendix contains various data which are of value in interpreting and understanding statements made in the previous chapters. The appendix is arranged in the following fashion:

1) Maps

A) The location of the study site in Santa Rosa National Park is within Costa Rica and Central America.

B) The study site, depicting the forest types and the locations of the grids used to sample the ecological conditions.

2) Climate Data

A) Monthly total rainfall for the periods of study in 1984 and 1985.

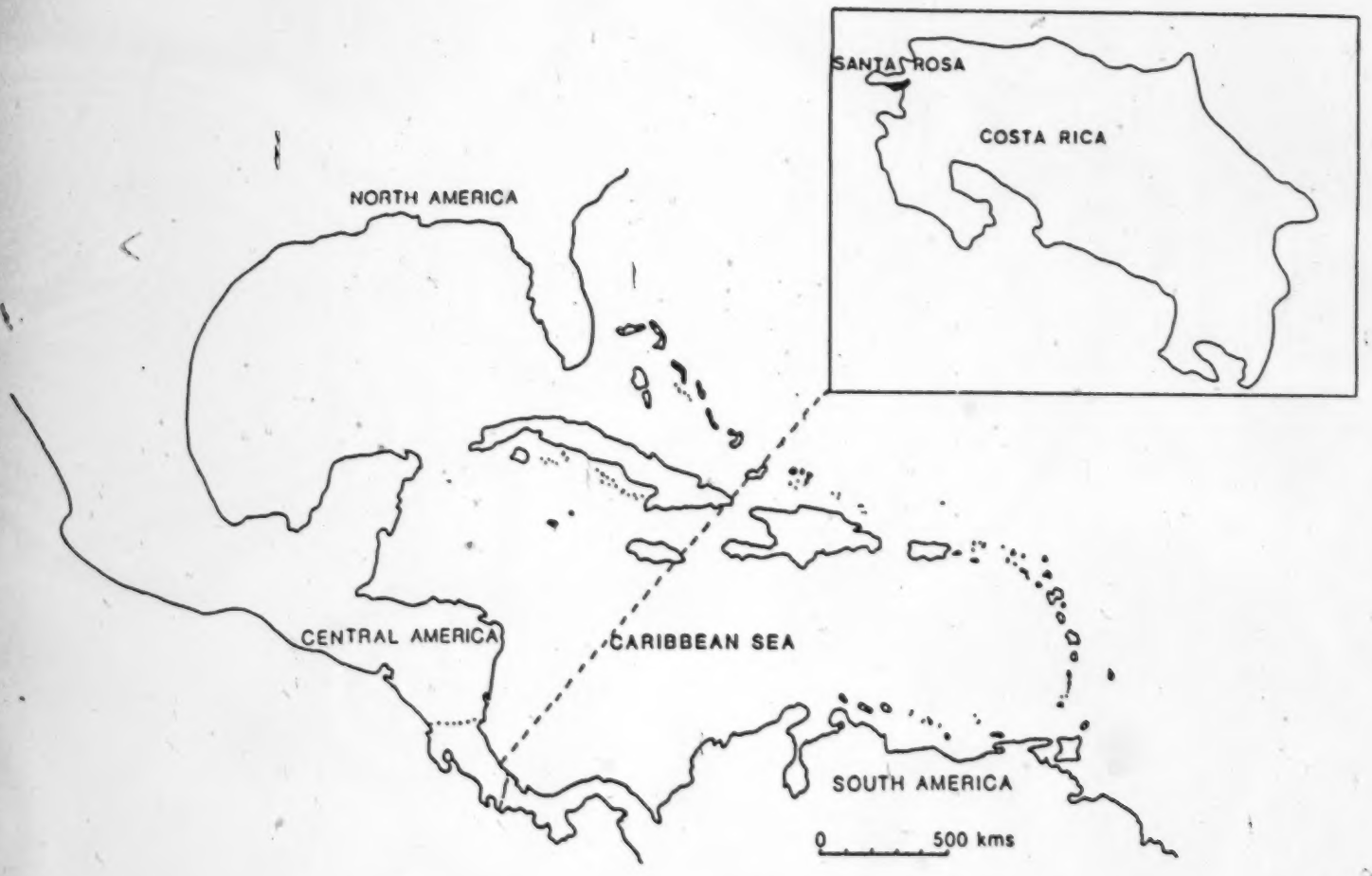
B) Monthly maximum and minimum temperatures for the period of study in 1984 and 1985.

C) Monthly maximum and minimum temperatures for wet and dry forest sites.

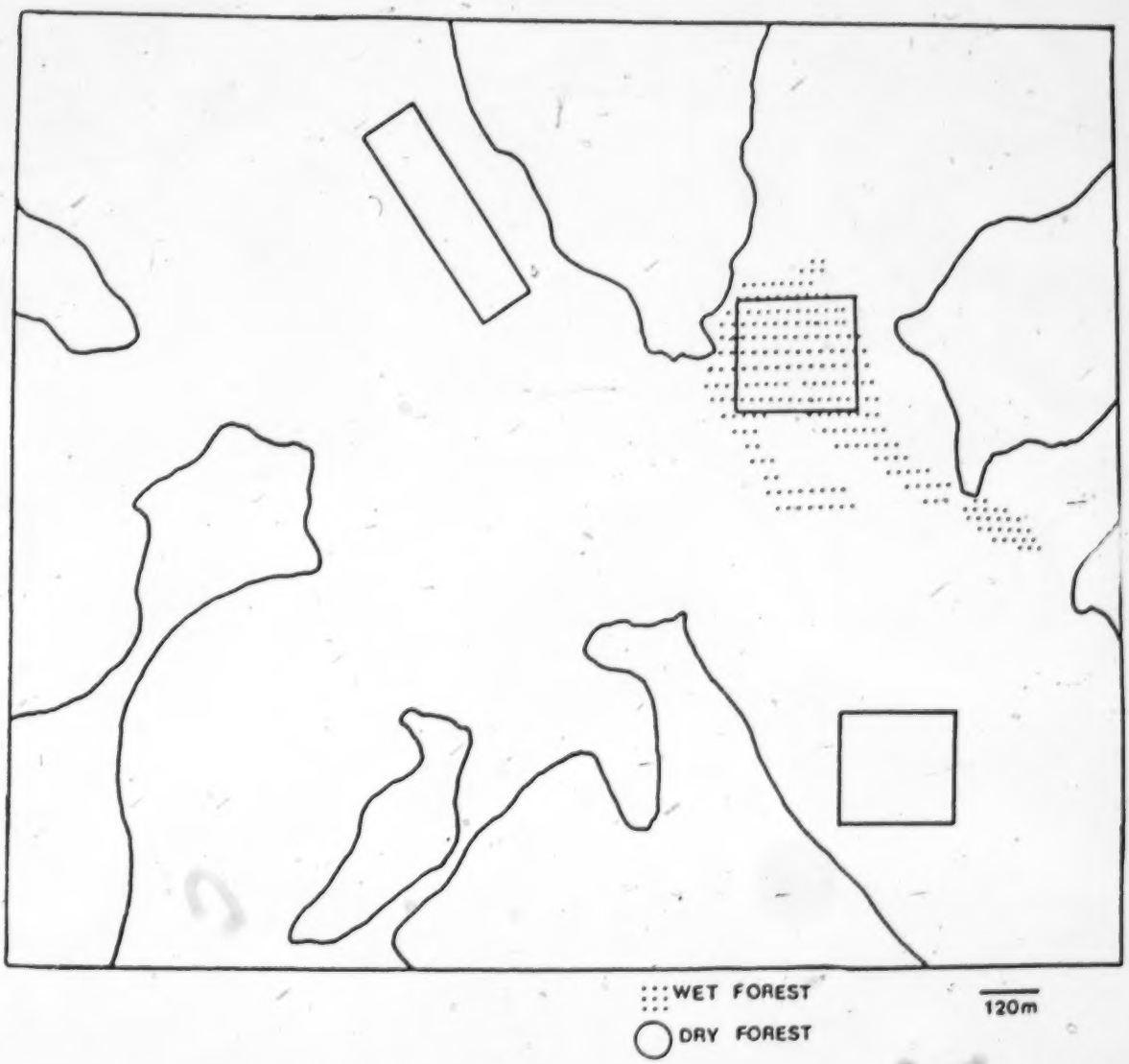
3) A description of various characteristics of the major plant species used by each of the three species of primates.

4) The location of sightings of individually recognizable spider monkeys and their corresponding home range.

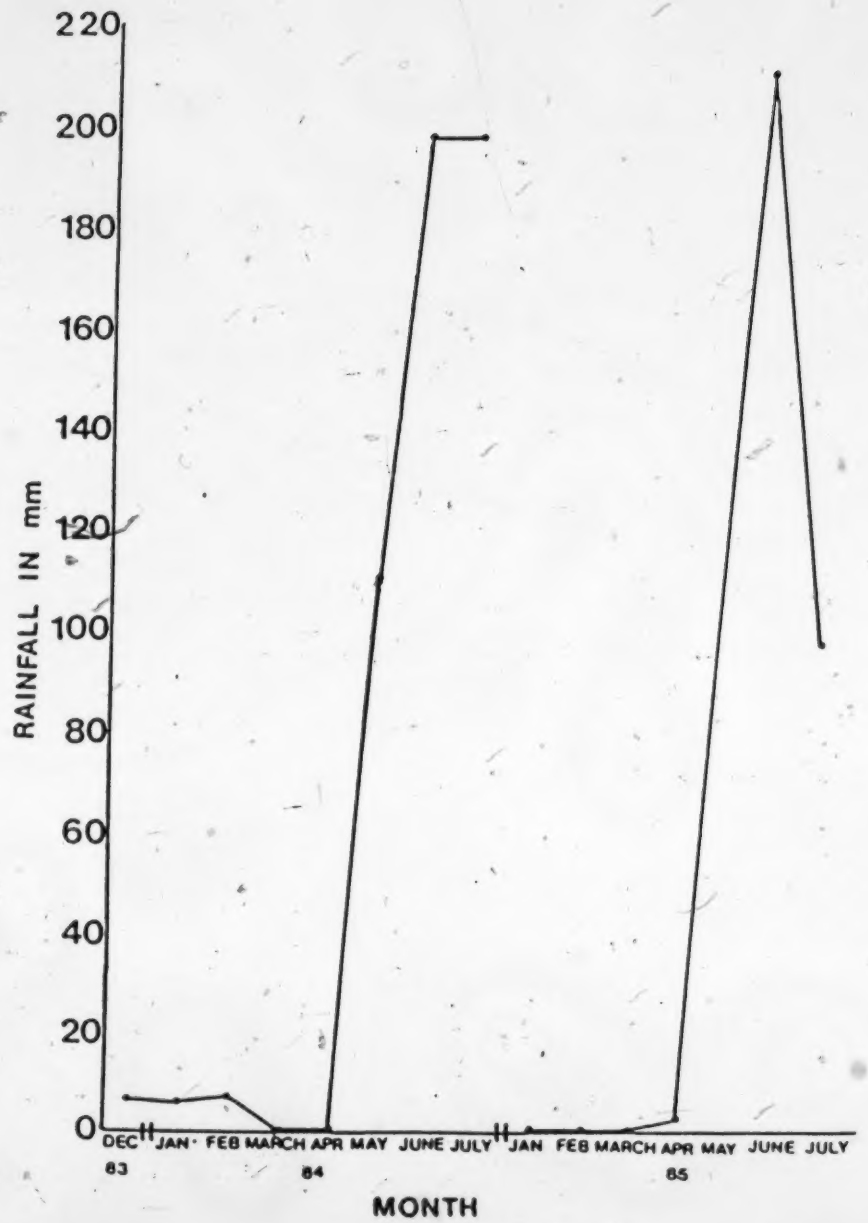
5) The availability of Muntingia calabura fruit and the corresponding use of this fruit by spider monkeys.



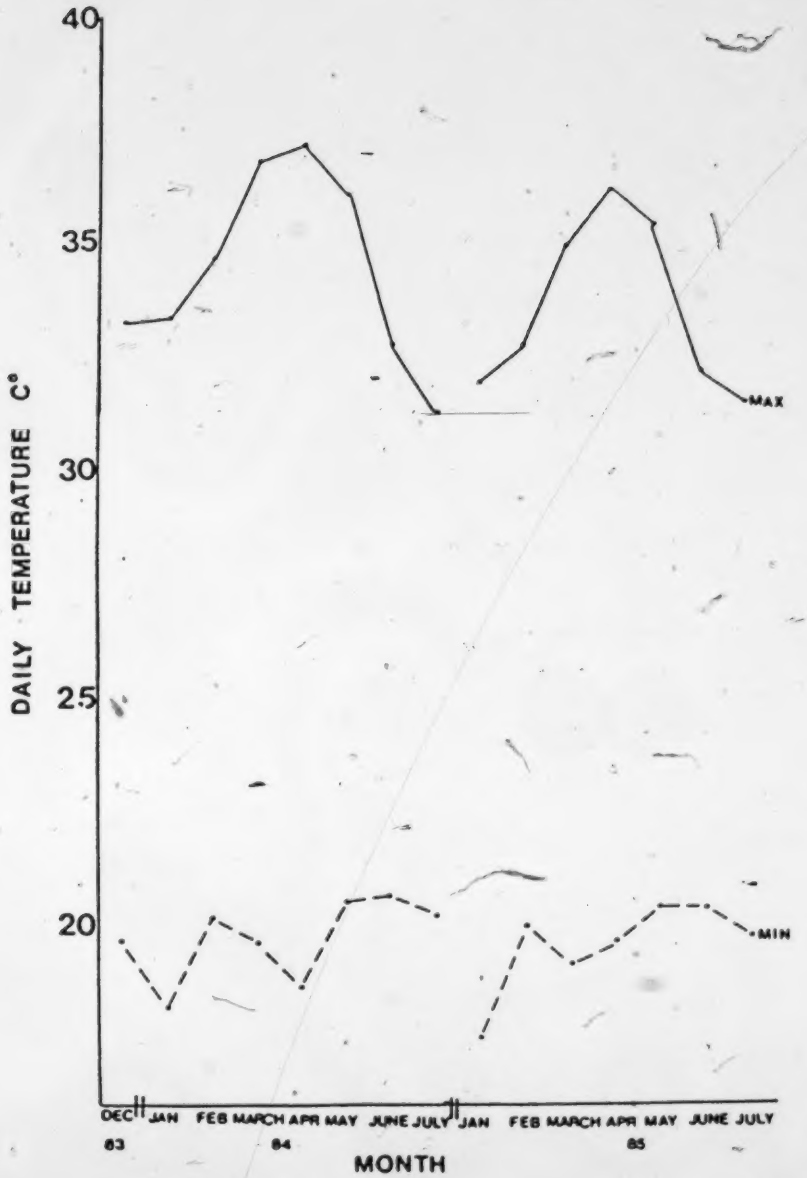
1A) The location of the study site, Santa Rosa National Park, within Costa Rica and Central America (adapted from "Dents Canadian Atlas" 1969).



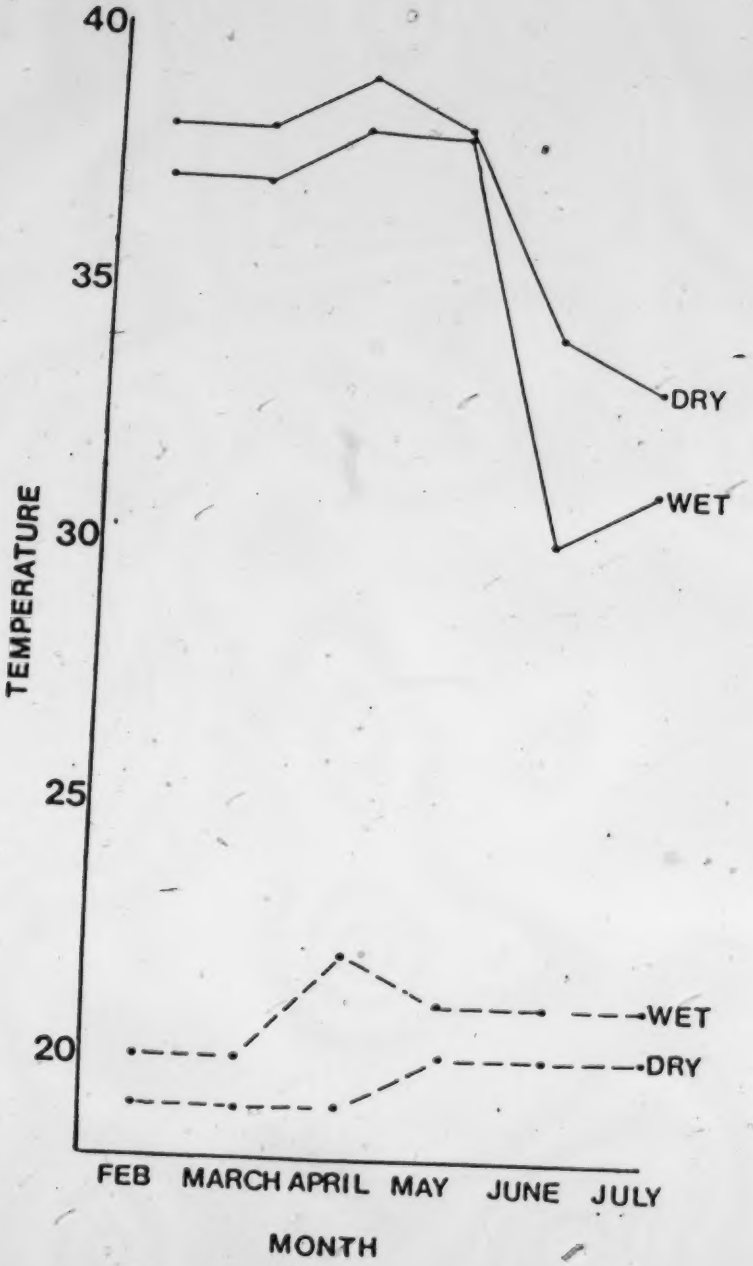
1B) The area in which the study species Ateles geoffrovi, Alouatta palliata, and Cebus capucinus were studied within Santa Rosa National Park, Costa Rica. The three boxes represent the location of the three 4-hectare grids used to sample the ecological conditions of interest. The shaded area represents the extent of semi-evergreen forest within the area.



2A) The total monthly rainfall in Santa Rosa National Park, Costa Rica during each month of the study in the 1984 and 1985 field seasons.



2B) The monthly maximum and minimum temperature in Santa Rosa National Park, Costa Rica during each month of the study in the 1984 and 1985 field seasons.



2C) The monthly maximum and minimum temperatures in semi-evergreen and dry deciduous forest sites in Santa Rosa National Park, Costa Rica. Eight maximum and minimum thermometers were placed in various locations, approximately 1.5 m off of the ground, in wet semi-evergreen forest and in dry decidous forest. Readings from the thermometers were taken on average once every 3 days during the 1985 field season.

3) A description of various characteristics of the major plant species used by the three species of primates in Santa Rosa National Park, Costa Rica (Ateles geoffroyi, Alouatta palliata, Cebus capucinus). Plant classification as per D.H. Janzen and R. Liesner. 1980. Annotated - list of plants of lowland Guanacaste Province, Costa Rica, exclusive of grasses and non-vascular cryptogams. Brenesia 18:15-90.
See the last page for a description of the variables used.

Family - Anacardiaceae
Plant - Spondias mombin
Density - 29.3 Individuals/hectare
Mean DBH - 19.4 cm
Predominate Forest Type - Dry

Part - Fruit	Spiders	Cebus	Howler
# of Months Available - 1			
% of Feeding Time	<1%	<1%	<1%
Selectivity	____	____	____
# of Months Used	____	____	____
Mean Feeding Time/Month	____	____	____
Range in Use/Month	____	____	____
CV in Use	____	____	____

Plant - Spondias purpurea
Density - 0.7 Individuals/hectare
Mean DBH - 17.1 cm
Predominate Forest Type - Dry

Part - Fruit	Spiders	Cebus	Howler
# of Months Available - 3			
% of Feeding Time	<1%	____	____
Selectivity	____	____	____
# of Months Used	____	____	____
Mean Feeding Time/Month	____	____	____
Range in Use/Month	____	____	____
CV in Use	____	____	____

Family - Araliaceae
Plant - Sciadodendron excelsum
Density - 0.7 Individuals/hectare
Mean DBH - 43.0 cm
Predominate Forest Type - Wet/Dry

Part - Fruit	Spiders	Cebus	Howler
# of Months Available - 2			
% of Feeding Time	<1%	2.50%	<1%
Selectivity	____	____	____
# of Months Used	____	2	____
Mean Feeding Time/Month	____	2.6	____
Range in Use/Month	____	0-28.1	____
CV in Use	____	311.5	____

Family - Bignoniaceae
Plant - Tabebuia ochracea
Density - 2.7 Individuals/hectare
Mean DBH - 20.8 cm
Predominate Forest Type - Dry

Part - Flower	Spiders	Cebus	Howler

# of Months Available - 1			
% of Feeding Time	2.84%	<1%	<1%
Selectivity	1.05		
# of Months Used	1	____	____
Mean Feeding Time/Month	6.14	____	____
Range in Use/Month	0-12.7	____	____
CV in Use	85.1	____	____

Family - Burseraceae
Plant - Bursera simaruba
Density - 20.8 individuals/hectare
Mean DBH - 20.4 cm
Predominate Forest Type - Dry

Part - Fruit	Spiders	Cebus	Howler
# of Months Available - 4			
% of Feeding Time	2.43%	1.30%	2.40%
Selectivity	0.12	0.06	0.12
# of Months Used	3	2	3
Mean Feeding Time/Month	12.2	1.10	2.20
Range in Use/Month	0-21.8	0-10.8	0-15.8
CV in Use	84.3	281.8	213.6

Part - Flowers	Spiders	Cebus	Howler
# of Months Available - 4			
% of Feeding Time	<1%	<1%	2.70%
Selectivity	____	____	0.13
# of Months Used	____	____	1
Mean Feeding Time/Month	____	____	1.1
Range in Use/Month	____	____	0-39.1
CV in Use	____	____	225.0

Part - Mature Leaves	Spiders	Cebus	Howler
# of Months Available - 8			
% of Feeding Time	____	____	3.81%
Selectivity	____	____	0.18
# of Months Used	____	____	3
Mean Feeding Time/Month	____	____	5.2
Range in Use/Month	____	____	0-39.1
CV in Use	____	____	225.0

Family - Caesalpinaceae
Plant - Hymenaea couraril
Density - 12.5 individuals/hectare
Mean DBH - ??? cm
Predominate Forest Type - Wet

Part - Leaf Buds	Spiders	Cebus	Howler
# of Months Available - 1			
% of Feeding Time	1.96%	____	2.62%
Selectivity	0.16	____	0.21
# of Months Used	1	____	3
Mean Feeding Time/Month	42.7	____	7.3
Range in Use/Month	0-86.3	____	0-70.0
CV in Use	99.2	____	276.7

Plant - Swartzia cubensis

Density - 0.08 Individuals/hectare
Mean DBH - 73.0 cm
Predominate Forest Type - Wet

Part - Fruit	Spiders	Cebus	Howler
# of Months Available - 1			
% of Feeding Time	1.10%	<1%	1.60%
Selectivity	13.8	____	20.0
# of Months Used	1	____	1
Mean Feeding Time/Month	5.6	____	1.0
Range in Use/Month	0-43.0	____	0-11.7
CV in Use	32.8	____	340.0

Family - Chrysobalanaceae
Plant - Licania arborea
Density - 1.3 Individuals/hectare
Mean DBH - 40.1 cm
Predominate Forest Type - Wet/Dry

Part - Fruit	Spiders	Cebus	Howler
# of Months Available - 3			
% of Feeding Time	1.70%	<1%	<1%
Selectivity	1.31	____	____
# of Months Used	2	____	____
Mean Feeding Time/Month	13.6	____	____
Range in Use/Month	0-20.5	____	____
CV in Use	71.8	____	____

Family - Elaeocarpaceae
Plant - Muntingia calabura
Density - 0.3 Individuals/hectare
Mean DBH - 18.3 cm
Predominate Forest Type - Wet/Dry

Part - Fruit	Spiders	Cebus	Howler
# of Months Available - 8			
% of Feeding Time	16.1%	17.9%	<1%
Selectivity	53.7	59.6	____
# of Months Used	7	7	____
Mean Feeding Time/Month	19.3	15.6	____
Range in Use/Month	0-45.1	0-31.1	____
CV in Use	77.4	285.7	____

Plant - Sloanea terniflora
Density - 2.3 Individuals/hectare
Mean DBH - 39.3 cm
Predominate Forest Type - Wet

Part - Fruit	Spiders	Cebus	Howler
# of Months Available - 5			
% of Feeding Time	2.19%	34.1%	<1%
Selectivity	0.95	14.8	____
# of Months Used	2	4	____
Mean Feeding Time/Month	3.5	19.0	____
Range in Use/Month	0-40.5	0-86.8	____
CV in Use	334.3	151.5	____

Family - Fabaceae
Plant - Lonchocarpus costaricensis
Density - 0.2 Individuals/hectare

Mean DBH - 47.5 cm
Predominate Forest Type - Dry

Part - Flowers	Spiders	Cebus	Howler
# of Months Available - 2			
% of Feeding Time	<1%	____	5.2%
Selectivity	____	____	26.0
# of Months Used	____	____	2
Mean Feeding Time/Month	____	____	6.8
Range in Use/Month	____	____	0-43.8
CV in Use	____	____	270.4

Family - Fagaceae
Plant - Quercus oleoides
Density - 5.0 individuals/hectare
Mean DBH - 57.3 cm
Predominate Forest Type - Wet/Dry

Part - Fruit	Spiders	Cebus	Howler
# of Months Available - 8			
% of Feeding Time	____	3.5%	____
Selectivity	____	0.7	____
# of Months Used	____	1	____
Mean Feeding Time/Month	____	4.5	____
Range in Use/Month	____	0-31.7	____
CV in Use	____	213.3	____

Family - Flacourtiaceae
Plant - Zuelania guidonia
Density - 0.8 individuals/hectare
Mean DBH - 27.6 cm
Predominate Forest Type - Wet

Part - Fruit	Spiders	Cebus	Howler
# of Months Available - 3			
% of Feeding Time	<1%	1.7%	<1%
Selectivity	____	2.1	____
# of Months Used	____	1	____
Mean Feeding Time/Month	____	1.1	____
Range in Use/Month	____	0-6.5	____
CV in Use	____	209.1	____

Family - Guttiferae
Plant - Rheedia edulis
Density - 0.2 individuals/hectare
Mean DBH - 10.8 cm
Predominate Forest Type - Wet

Part - Fruit	Spiders	Cebus	Howler
# of Months Available - 2			
% of Feeding Time	<1%	<1%	<1%
Selectivity	____	____	____
# of Months Used	____	____	____
Mean Feeding Time/Month	____	____	____
Range in Use/Month	____	____	____
CV in Use	____	____	____

Family - Lauraceae
Plant - Ocotea verguensis
Density - 7.1 individuals/hectare

Mean DBH - 15.1 cm
Predominate Forest Type - Wet

Part - Fruit	Spiders	Cebus	Howler
# of Months Available - 4			
% of Feeding Time	1.29%	1.1%	<1%
Selectivity	0.18	0.15	____
# of Months Used	3	2	____
Mean Feeding Time/Month	4.4	1.7	____
Range in Use/Month	0-9.1	0-19.4	____
CV in Use	86.8	329.4	____

Family - Mimosaceae
Plant - Inga vera
Density - 0.2 Individuals/hectare
Mean DBH - 22.5 cm
Predominate Forest Type - Wet

Part - Fruit	Spiders	Cebus	Howler
# of Months Available - 2			
% of Feeding Time	<1%	<1%	<1%
Selectivity	____	____	____
# of Months Used	____	____	____
Mean Feeding Time/Month	____	____	____
Range in Use/Month	____	____	____
CV in Use	____	____	____

Plant - Pithecellobium saman
Density - 0.8 Individuals/hectare
Mean DBH - 47.8 cm
Predominate Forest Type - Wet/Dry

Part - Flowers	Spiders	Cebus	Howler
# of Months Available - 4			
% of Feeding Time	2.85%	<1%	6.8%
Selectivity	3.56	____	8.5
# of Months Used	3	____	3
Mean Feeding Time/Month	10.3	____	6.8
Range in Use/Month	0-16.1	____	0-51.7
CV in Use	148.8	____	227.9

Part - Mature Leaves	Spiders	Cebus	Howler
# of Months Available - 8			
% of Feeding Time	<1%	<1%	1.8%
Selectivity	____	____	2.25
# of Months Used	____	____	3
Mean Feeding Time/Month	____	____	3.9
Range in Use/Month	____	____	0-39.1
CV in Use	____	____	287.2

Family - Moraceae
Plant - Brosimum alicastrum
Density - 0.8 Individuals/hectare
Mean DBH - 29.9 cm
Predominate Forest Type - Wet

Part - Fruit	Spiders	Cebus	Howler
# of Months Available - 2			
% of Feeding Time	2.73%	<1%	5.50%
Selectivity	3.41	____	4.04

# of Months Used	2	____	2
Mean Feeding Time/Month	9.88	____	3.20
Range in Use/Month	0-15.1	____	0-36.8
CV in Use	53.7	____	311.3

Part - Young Leaves	Spiders	Cebus	Howler
# of Months Available - 3			
% of Feeding Time	<1%	____	1.10%
Selectivity	____	____	1.38
# of Months Used	____	____	2
Mean Feeding Time/Month	____	____	1.1
Range in Use/Month	____	____	1.7.7
CV in Use	____	____	236.4

Plant - Castilla elastica
Density - 4.1 Individuals/hectare
Mean DBH - 19.7 cm
Predominate Forest Type - Wet

Part - Leaf Buds	Spiders	Cebus	Howler
# of Months Available - 2			
% of Feeding Time	<1%	____	2.4%
Selectivity	____	____	0.59
# of Months Used	____	____	3
Mean Feeding Time/Month	____	____	2.9
Range in Use/Month	____	____	0-11.1
CV in Use	____	____	193.1

Plant - Cecropia peltata
Density - 7.7 Individuals/hectare
Mean DBH - 21.9 cm
Predominate Forest Type - Dry

Part - Fruit	Spiders	Cebus	Howler
# of Months Available - 5			
% of Feeding Time	1.12%	<1%	<1%
Selectivity	0.15	____	____
# of Months Used	5	____	____
Mean Feeding Time/Month	2.29	____	____
Range in Use/Month	0-5.1	____	____
CV in Use	93.1	____	____

Plant - Chlorophora tinctoria
Density - 2.17 Individuals/hectare
Mean DBH - 28.7 cm
Predominate Forest Type - Dry

Part - Fruit	Spiders	Cebus	Howler
# of Months Available - 2			
% of Feeding Time	<1%	____	____
Selectivity	____	____	____
# of Months Used	____	____	____
Mean Feeding Time/Month	____	____	____
Range in Use/Month	____	____	____
CV in Use	____	____	____

Plant - *Ficus* sp.
Density - 0.6 Individuals/hectare
Mean DBH - 110.9 cm
Predominate Forest Type - Dry/Wet

Part - Fruit	Spiders	Cebus	Howler
# of Months Available - 5			
% of Feeding Time	29.1%	1.9%	15.5%
Selectivity	48.5	3.17	13.3
# of Months Used	5	5	5
Mean Feeding Time/Month	32.5	4.1	8.0
Range in Use/Month	0-72.4	0-30.1	0-39.5
CV in Use	65.1	231.7	169.5

Part - Young Leaves	Spiders	Cebus	Howler
# of Months Available - 5			
% of Feeding Time	2.37%	2.40%	5.24%
Selectivity	4.55	4.0	8.73
# of Months Used	2	1	1
Mean Feeding Time/Month	8.9	1.7	5.2
Range in Use/Month	0-16.4	____	0-62.2
CV in Use	120.3	____	346.2

Part - Leaf Buds	Spiders	Cebus	Howler
# of Months Available - 4			
% of Feeding Time	<1%	<1%	2.00%
Selectivity	____	____	3.33
# of Months Used	____	____	2
Mean Feeding Time/Month	____	____	3.64
Range in Use/Month	____	____	0-22.4
CV in Use	____	____	219.4

Part - Mature Leaves	Spiders	Cebus	Howler
# of Months Available - 8			
% of Feeding Time	<1%	____	1.6%
Selectivity	____	____	2.67
# of Months Used	____	____	1
Mean Feeding Time/Month	____	____	0.8
Range in Use/Month	____	____	0-7.7
CV in Use	____	____	275.0

Plant - *Trophis racemose*
Density - 0.3 Individuals/hectare
Mean DBH - 22.3 cm
Predominate Forest Type - Wet

Part - Fruit	Spiders	Cebus	Howler
# of Months Available - 2			
% of Feeding Time	<1%	<1%	<1%
Selectivity	____	____	____
# of Months Used	____	____	____
Mean Feeding Time/Month	____	____	____
Range in Use/Month	____	____	____
CV in Use	____	____	____

Family - Polygonaceae
Plant - *Coccoloba venosa*

Density - ?? Individuals/hectare
Mean DBH - ?? cm
Predominate Forest Type - Wet/Dry

Part - Fruit	Spiders	Cebus	Howler
# of Months Available - 2			
% of Feeding Time	2.74%		
Selectivity			
# of Months Used	2		
Mean Feeding Time/Month	7.54		
Range in Use/Month	0-17.7		
CV in Use	115.0		

Family - Rubiaceae
Plant - Genipa americana
Density - 0.8 Individuals/hectare
Mean DBH - 20.8 cm
Predominate Forest Type - Dry

Part - Fruit	Spiders	Cebus	Howler
# of Months Available - 4			
% of Feeding Time	<1%	<1%	<1%
Selectivity			
# of Months Used			
Mean Feeding Time/Month			
Range in Use/Month			
CV in Use			

Plant - Randia echinocarpa
Density - 1.6 Individuals/hectare
Mean DBH - 9.7 cm
Predominate Forest Type - Dry

Part - Fruit	Spiders	Cebus	Howler
# of Months Available - 4			
% of Feeding Time	<1%	<1%	<1%
Selectivity			
# of Months Used			
Mean Feeding Time/Month			
Range in Use/Month			
CV in Use			

Family - Sapindaceae
Plant - Dipterodendron costaricensis
Density - 2.5 Individuals/hectare
Mean DBH - 17.5 cm
Predominate Forest Type - Wet

Part - Fruit	Spiders	Cebus	Howler
# of Months Available - 3			
% of Feeding Time	6.27%	1.30%	<1%
Selectivity	2.51	0.5	
# of Months Used	3	3	
Mean Feeding Time/Month	23.7	0.9	
Range in Use/Month	0-41.4	0-9.6	
CV in Use	148.5	311.1	

Family - Sapotaceae
Plant - Manilkara chicle
Density - 9.8 Individuals/hectare

Mean DBH - 29.4 cm
Predominate Forest Type - Wet

Part - Fruit	Spiders	Cebus	Howler
# of Months Available - 2			
% of Feeding Time	2.04%	<1%	2.7%
Selectivity	0.21	———	0.31
# of Months Used	2	———	1
Mean Feeding Time/Month	13.6	———	4.5
Range in Use/Month	0-31.5	———	0-30.0
CV in Use	130.1	———	215.6

Part - Flowers	Spiders	Cebus	Howler
# of Months Available - 2			
% of Feeding Time	1.19%	<1%	7.40%
Selectivity	0.12	———	0.76
# of Months Used	1	———	2
Mean Feeding Time/Month	5.8	———	4.7
Range in Use/Month	0-10.6	———	0-33.4
CV in Use	130.1	———	214.9

Plant - Mastichodendeon capiri
Density - 0.25 Individuals/hectare
Mean DBH - 49.8 cm
Predominate Forest Type - Wet

Part - Fruit	Spiders	Cebus	Howler
# of Months Available - 3			
% of Feeding Time	6.7%	<1%	3.1%
Selectivity	26.8	———	12.4
# of Months Used	3	———	3
Mean Feeding Time/Month	13.8	———	13.7
Range in Use/Month	2.0-42.2	———	0-30.2
CV in Use	0.89	———	1.1

Family - Simaroubaceae
Plant - Simaruba glauca
Density - 0.4 Individuals/hectare
Mean DBH - 14.0 cm
Predominate Forest Type - Dry

Part - Fruit	Spiders	Cebus	Howler
# of Months Available - 3			
% of Feeding Time	<1%	<1%	<1%
Selectivity	———	———	———
# of Months Used	———	———	———
Mean Feeding Time/Month	———	———	———
Range in Use/Month	———	———	———
CV in Use	———	———	———

Family - Tiliaeae
Plant - Luehea speciosa
Density - 19.9 Individuals/hectare
Mean DBH - 27.0 cm
Predominate Forest Type - Dry

Part - Fruit	Spiders	Cebus	Howler
# of Months Available - 8			
% of Feeding Time	———	4.4%	———
Selectivity	———	0.2	———

# of Months Used	____	2	____
Mean Feeding Time/Month	____	5.6	____
Range in Use/Month	____	0-56.1	____
CV in Use	____	285.7	____

Plant - Luehea candida
Density - 0.09 Individuals/hectare
Mean DBH - 71 cm
Predominate Forest Type - Dry

Part - Fruit	Spiders	Cebus	Howler
# of Months Available - 8			
% of Feeding Time		<1%	
Selectivity	____	____	____
# of Months Used	____	____	____
Mean Feeding Time/Month	____	____	____
Range in Use/Month	____	____	____
CV in Use	____	____	____

- Plants which were consumed for greater than 1% of the feeding time for any of the three primate species, plus any plants for which density was determined were included in this list

- # of Months Available = the number of months a food item was in a tree in the gridded areas or was fed on between January and August calculated as a mean for the three years

- CV in Use = Standard deviation in the % of the time spend feeding on that item when it was used expressed as a % of the mean

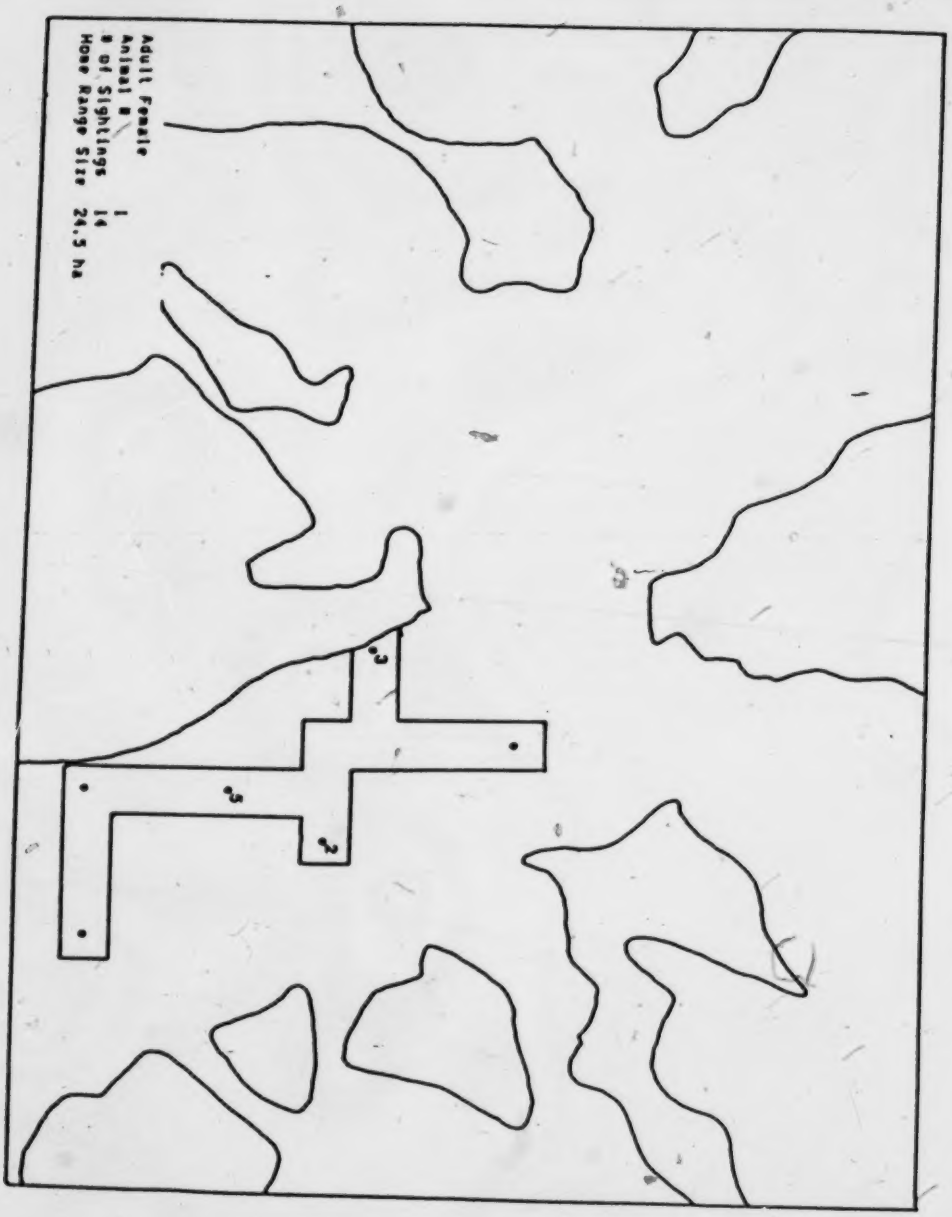
- Mean Feeding Time/Month = calculated from the percentage of feeding time spent eating on that item in each of the months that the item was used.

- Selectivity = % of feeding time/density

- Density was calculated from counts conducted in three 4-hectare grids. Each grid consisted of 400 cells that were 10 m by 10 m in size and each corner of the cell was marked with an individually labelled steel post. The grids encompassed 9.0% of both the cebus and howling monkeys home ranges. Each grid was established in different types of habitat, such that the major habitats used by the monkeys were sampled.

- The availability of food items were determined approximately once every 3 weeks by recording the phenological status of every individual adult tree in the grids.

4) The location of sightings of individually recognizable spider monkeys Ateles geoffroyi in Santa Rosa National Park, Costa Rica. The number of times (greater than one) that an animal was seen to use a 120 m by 120 m grid cell is depicted in the cell. A single dot in the center of the cell represents a single sighting. The home range size was calculated as the sum of the cells that the individual was seen to use or would have had to pass through to get from one observation point to another. The total home range, the number of sightings, and the animals age and sex class are outlined on the figures.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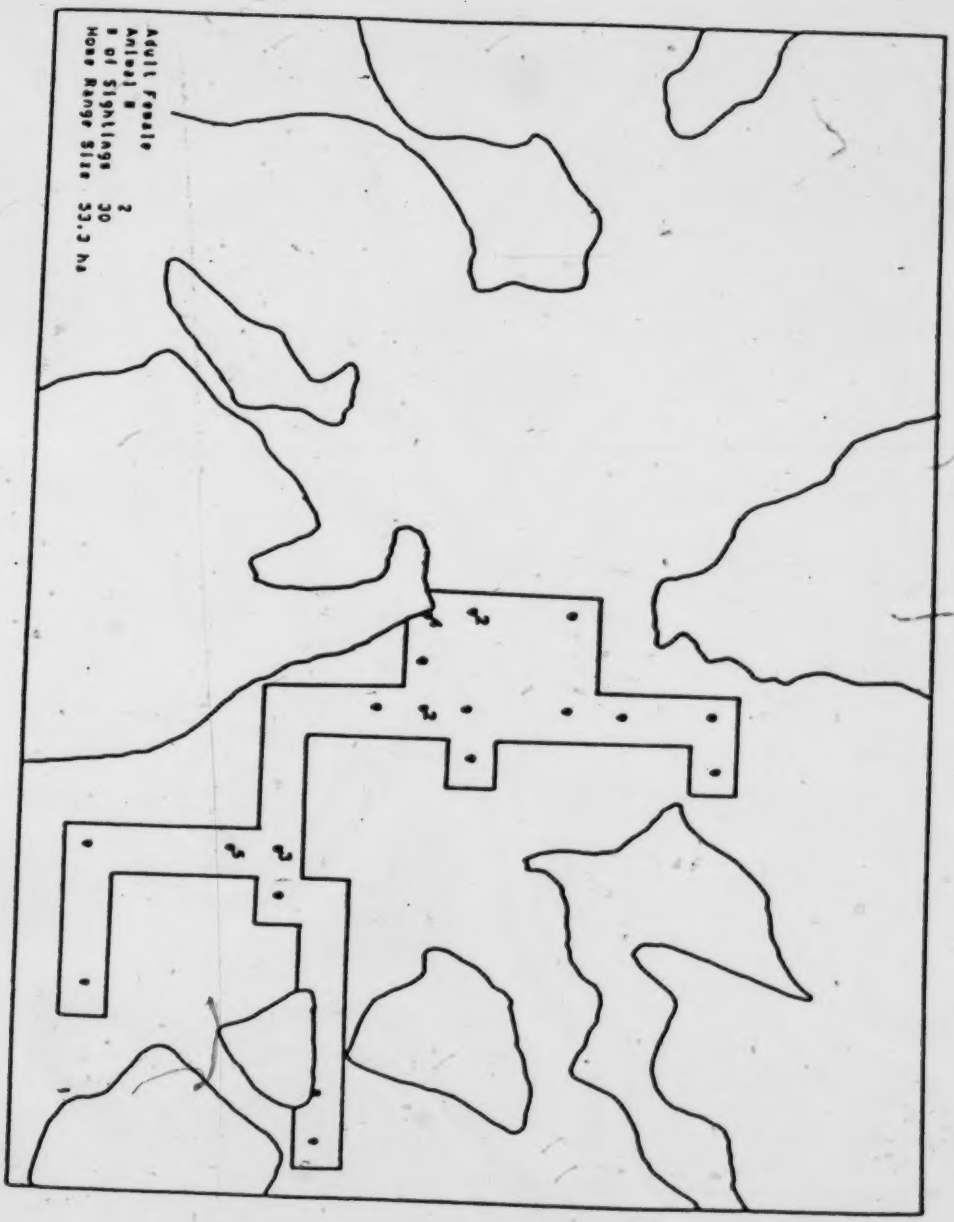
Animal #
# of Sightings 14
Home Range Size 24.5 ha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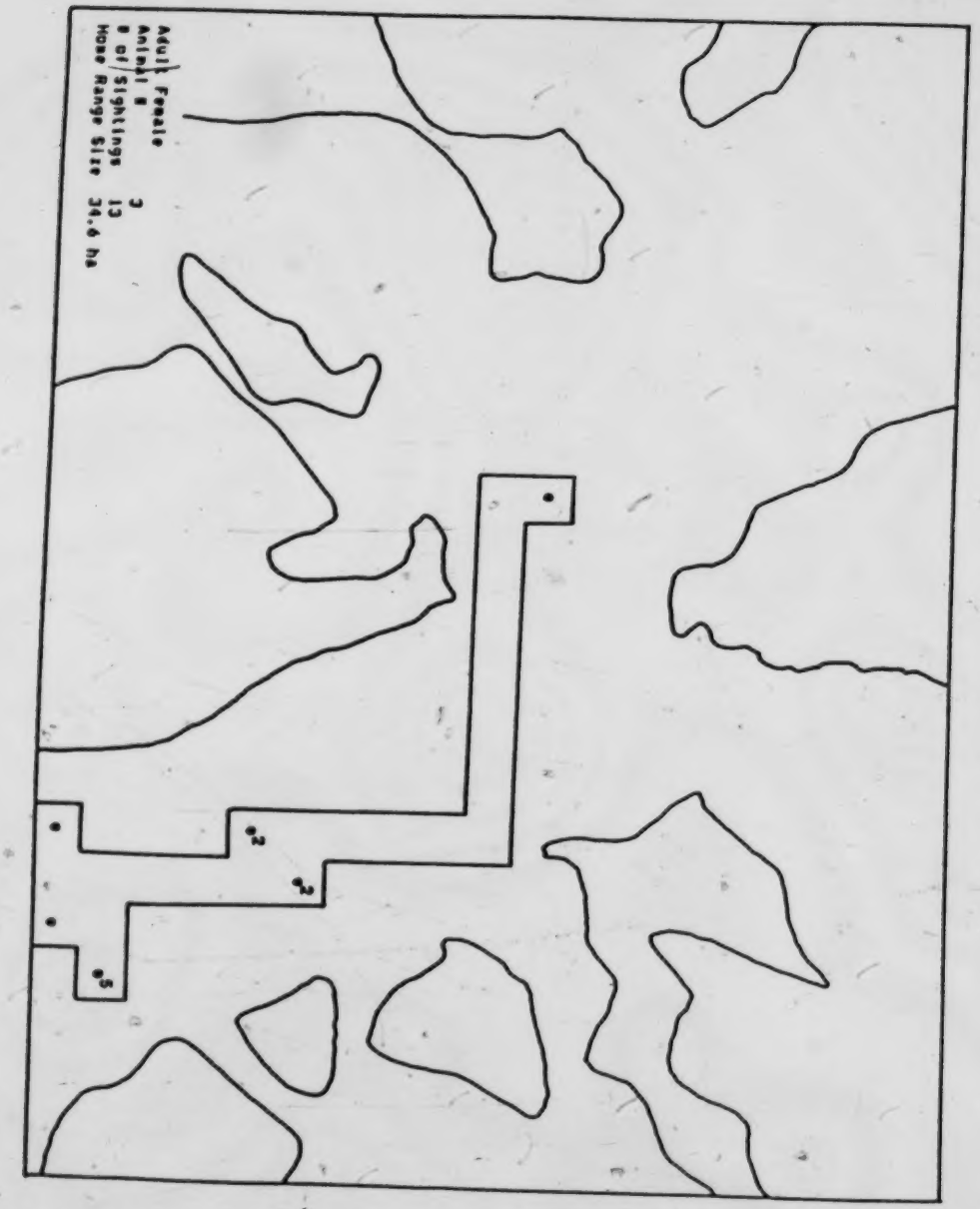
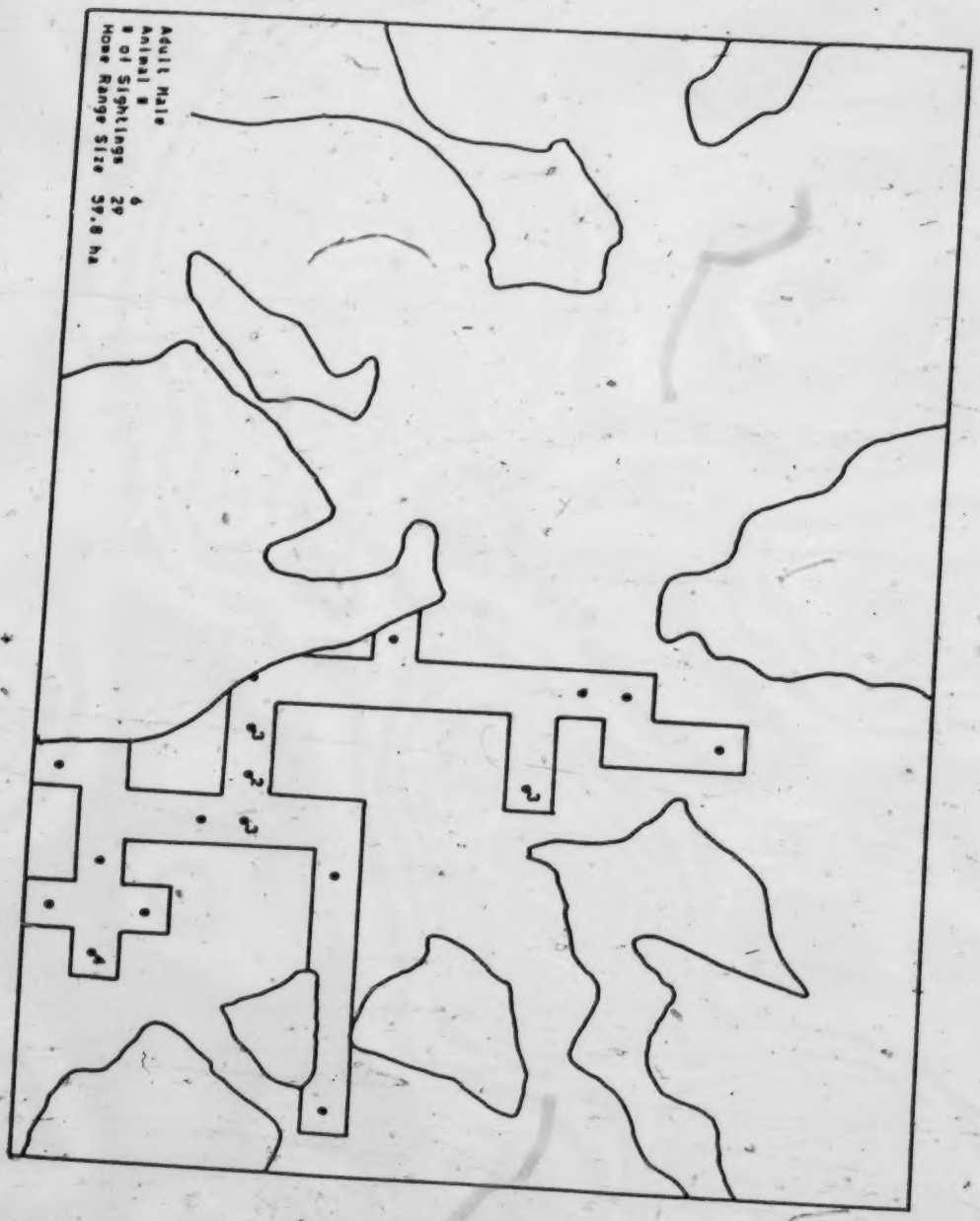
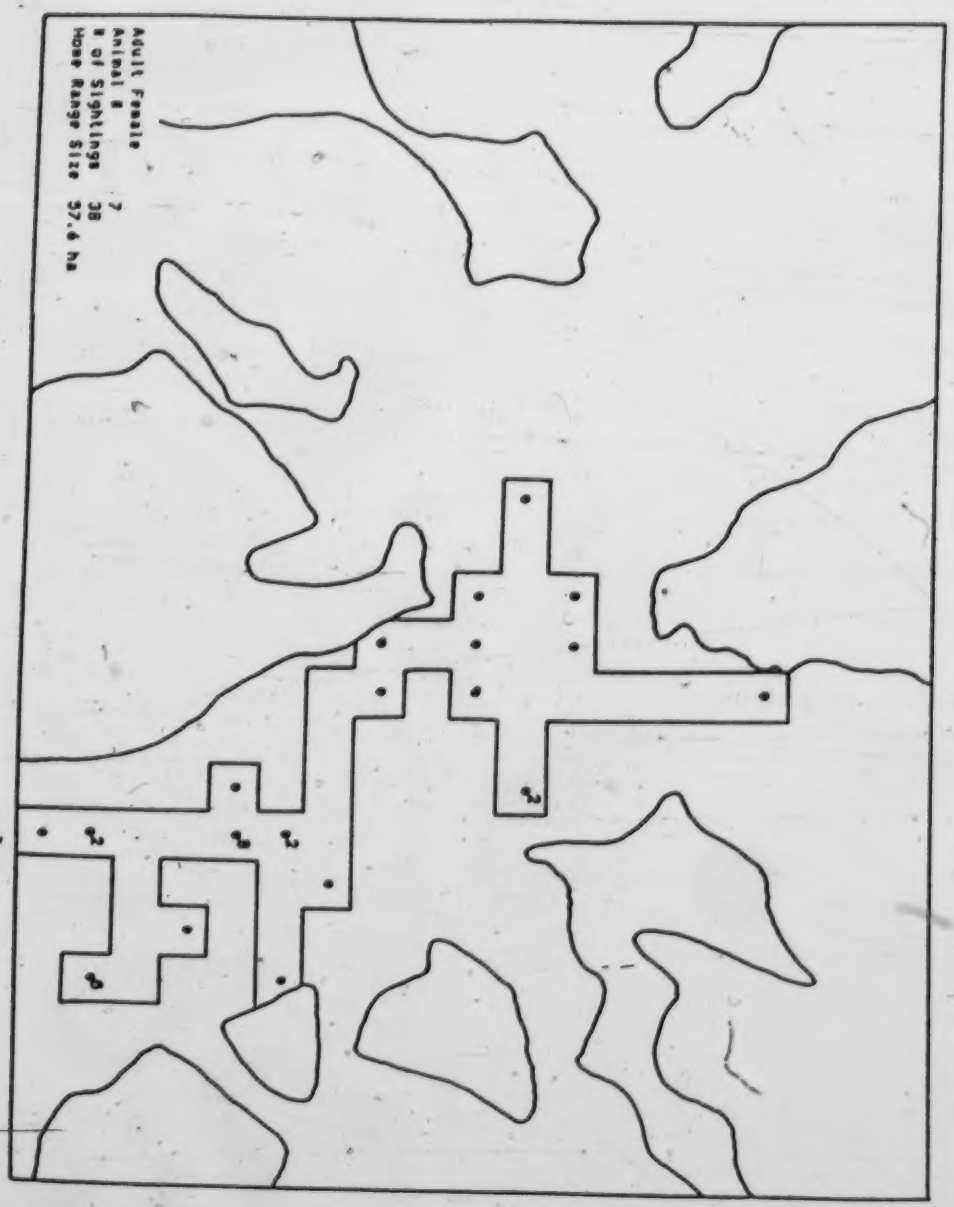
Animal #
# of Sightings 30
Home Range Size 33.3 Ha

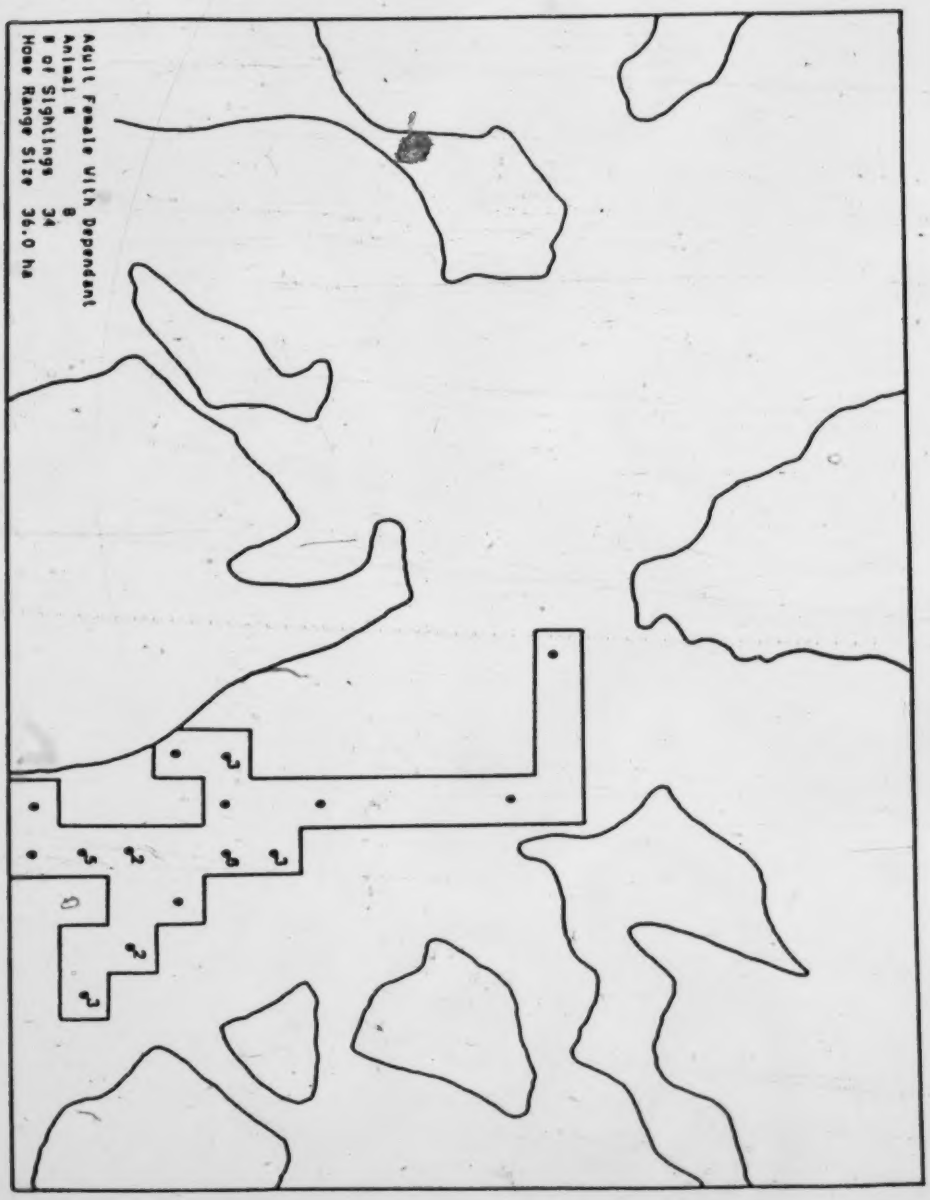

Adult Female
Animal #
# of Sightings 3
13
Home Range Size 34.6 Ha

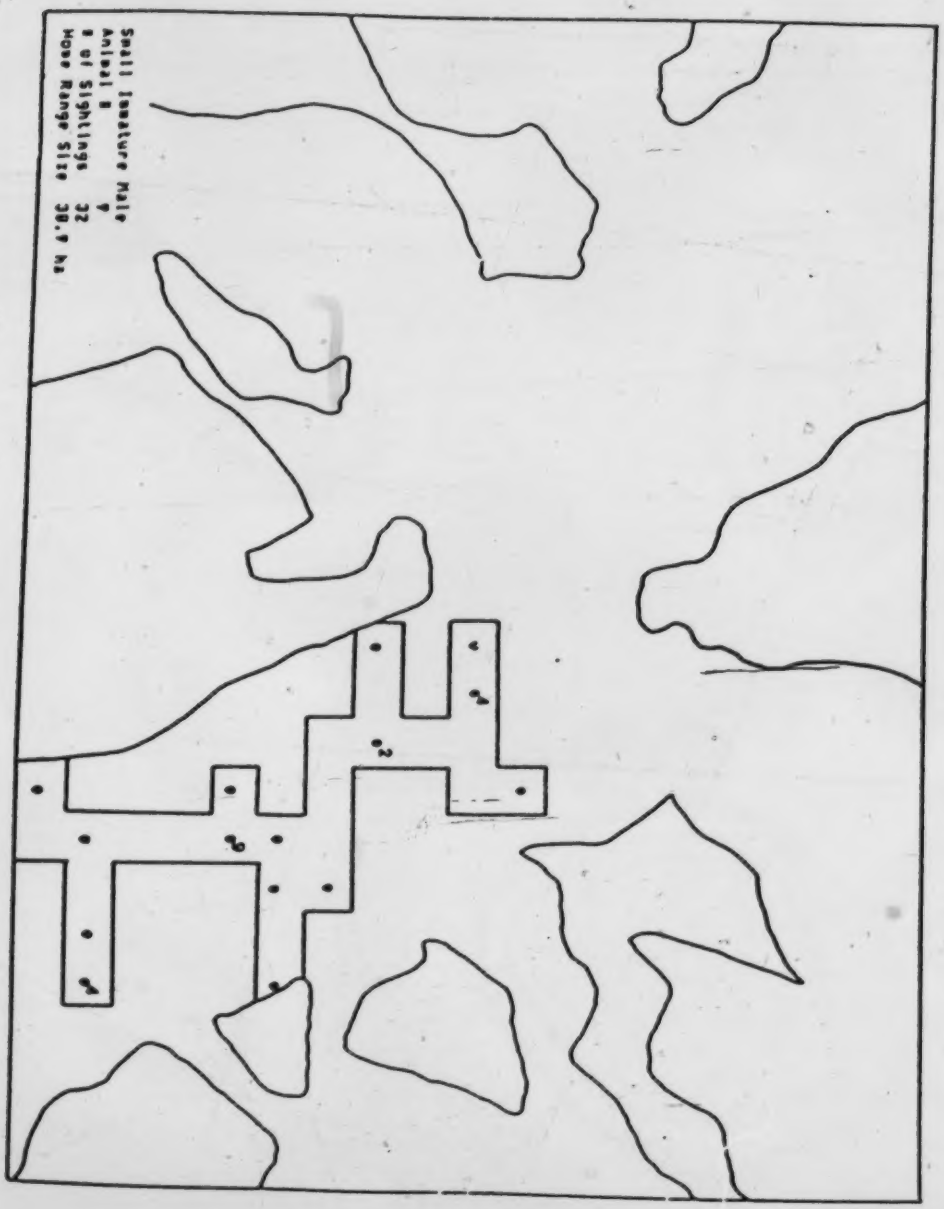
Adult Female With Dependant
Animal #
# of Sightings 54
Home Range Size 37.4 ha

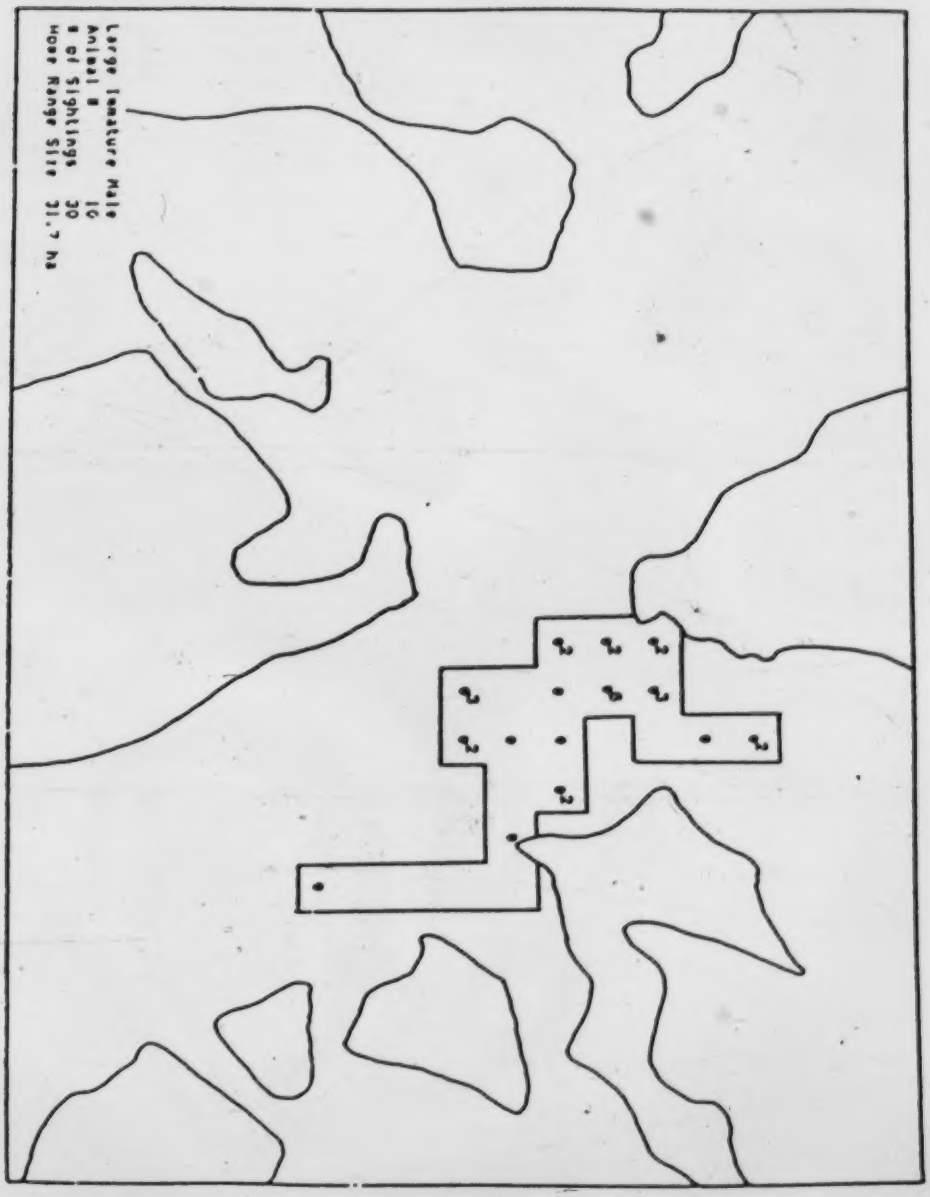

Adult Male
Animal 8
# of Sightings 6
2P
Home Range Size 59.8 Ha

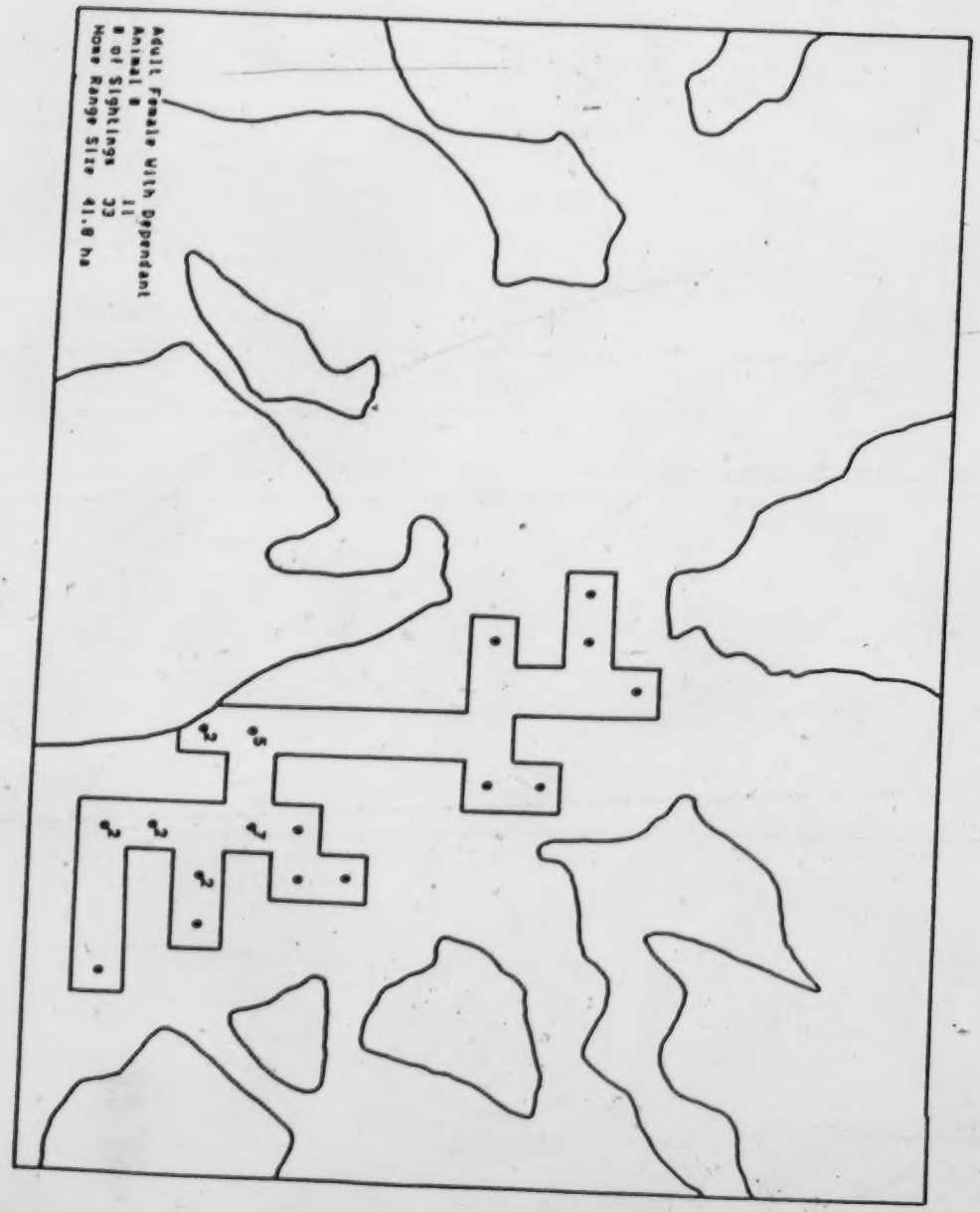
Large Immature Female
Animal #
3
# of Sightings
26
Home Range Size
49.0 ha

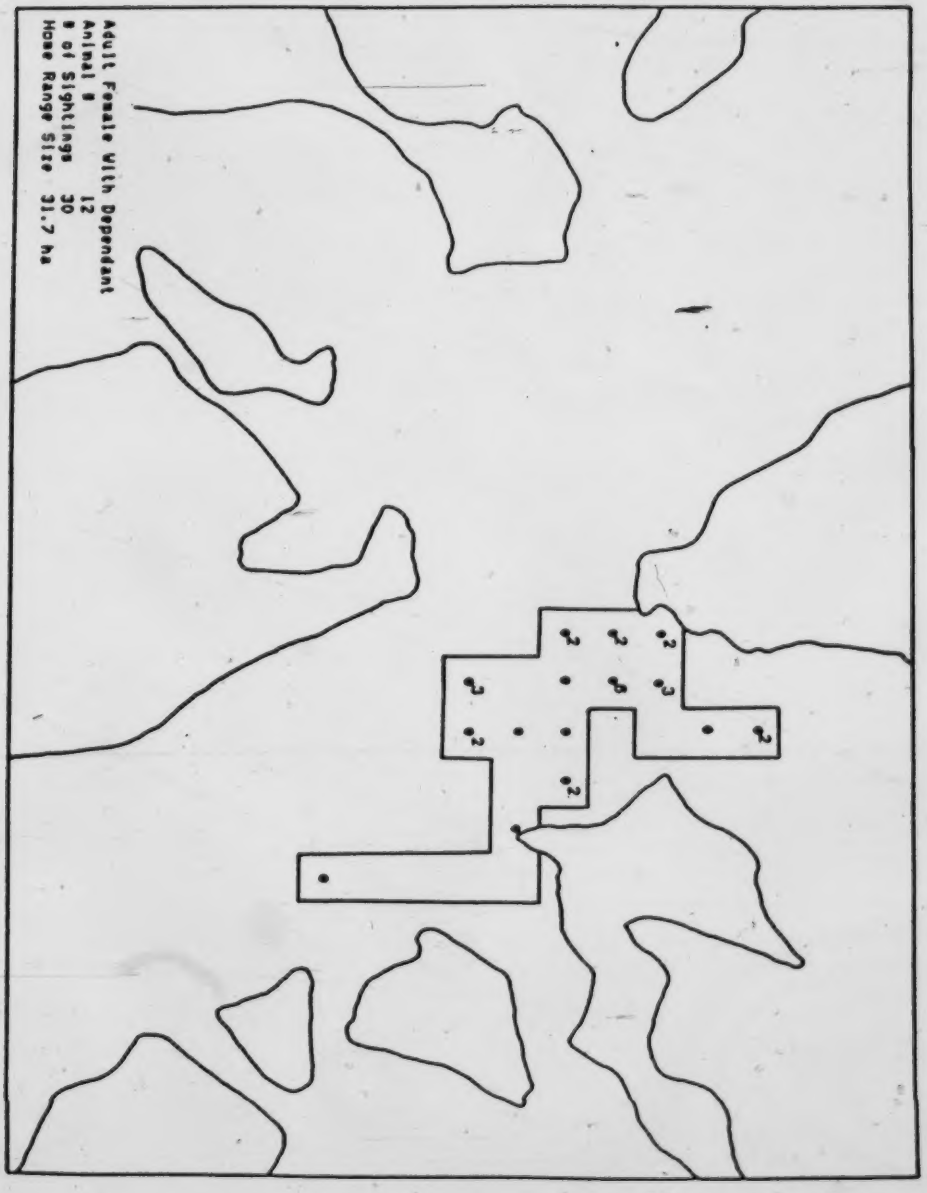

Adult Female
Animal #
# of Sightings 38
Home Range Size 37.6 ha

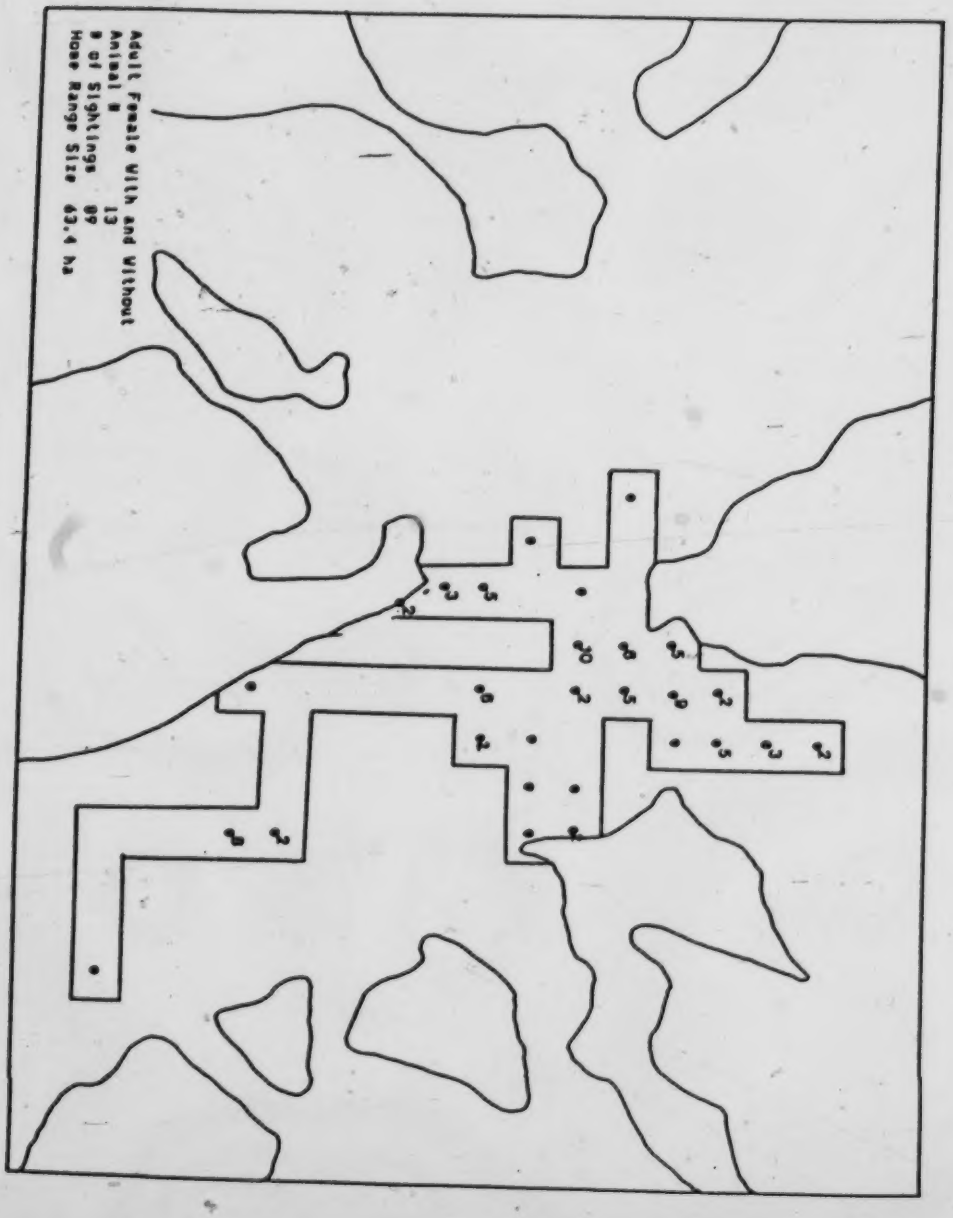

Adult Female With Dependent
Animal #
# of Sightings 34
Home Range Size 36.0 ha

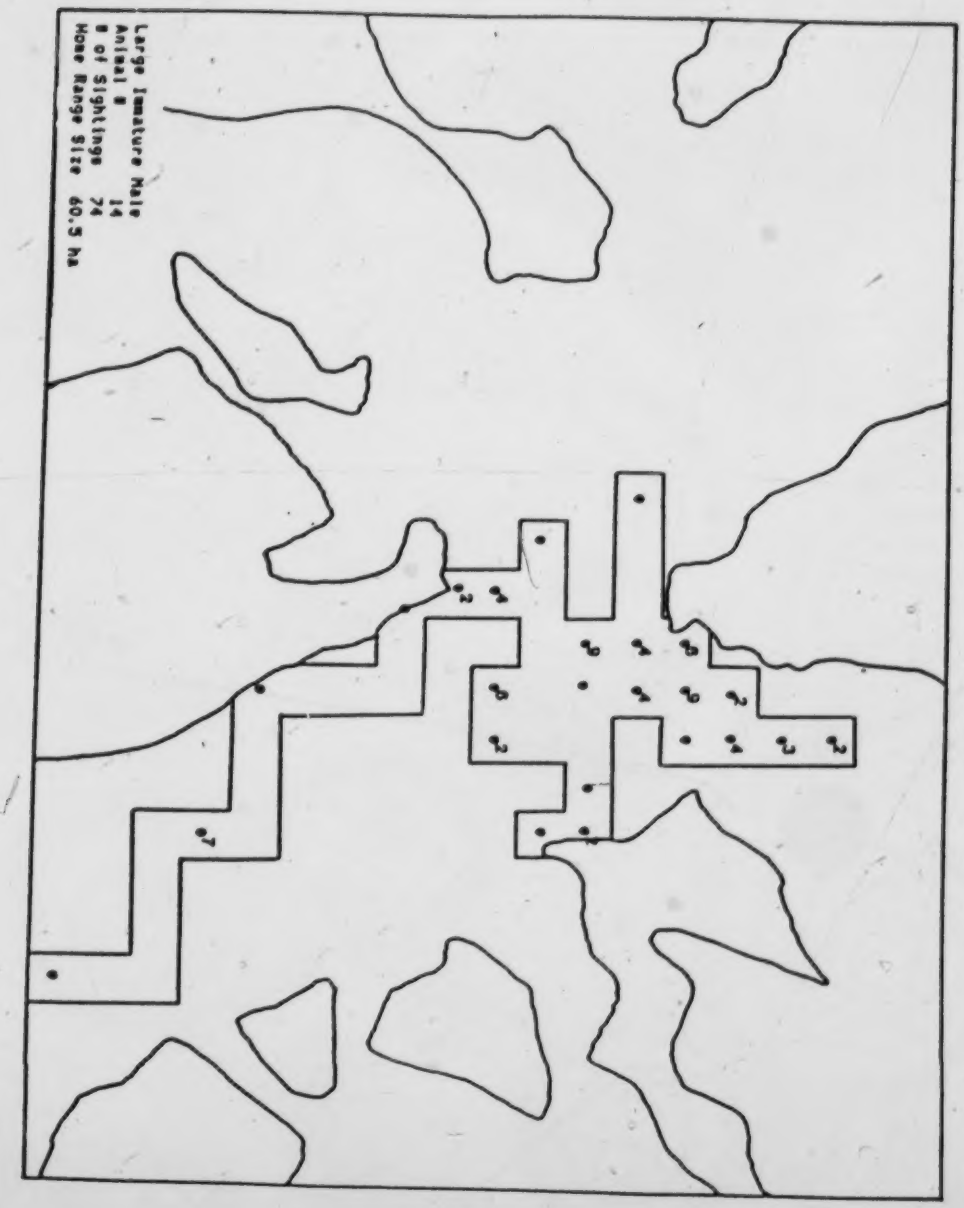

Small immature Male
Animal 8
# of Sightings 32
Home Range Size 38.8 ha

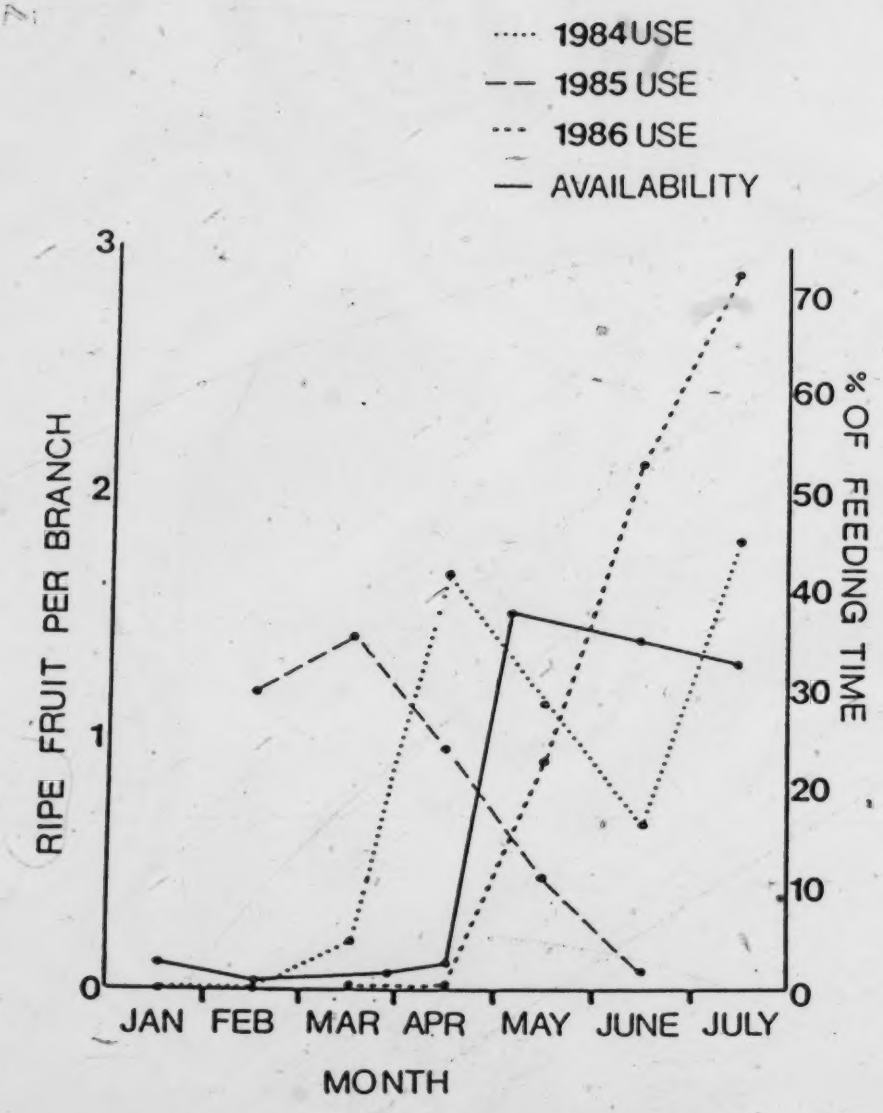

Large lenticular mass
of slightly
to
Average
Mean range size


Adult Female With Dependant
Animal #
# of Sightings 11
30
Home Range Size 41.8 Ha


Adult Female With Dependant
Animal #
# of Sightings 30
Home Range Size 31.7 ha


Adult Female With and Without
Animal #
# of Sightings
Home Range Size 63.4 ha


Large Immature Male
Animal #
# of Sightings
Home Range Size 60.5 Ha



5) The availability of fruits of Muntingia calabura between January and July and the corresponding level of exploitation by the spider monkeys (Ateles geoffroyi) of Santa Rosa National Park, Costa Rica. Availability was adapted from Fleming et al. 1985. These authors conducted a 10 year study of the phenology of M. calabura in Santa Rosa National Park and estimated the number of ripe frit per branch in each month of the year. The use of this food source by spider monkeys is represented as the proportion of their total feeding time in a month that was devoted to eating fruits of this tree. (Fleming, T.H., C.F. Williams, F.J. Bonaccorso, and L.H. Herbst. 1985. Phenology, seed dispersal, and colonization in Muntingia calabura, a neotropical pioneer tree. Amer. J. Bot. 72:383-391.

Appendix 2 : Fission-Fusion Societies in Mammals

Introduction

Past research on mammals has produced extensive documentation of the types of social organization found in this class. However, quantitative data on the compositional stability of social groups is lacking for most mammalian species. The paucity of information stems from the difficulty in identifying individuals.

A number of recent studies in which individual recognition of group members was possible, have described social organizations in which animals associate in loosely organized groups (subgroups or parties) that are unstable in size and composition, but which are organized on a higher community level. Because of the unstable nature of these groups, this type of social organization has been called a "fission-fusion society" (Anderson 1981, Fedigan 1982, Wrangham 1980, 1986, Rubenstein 1986). It is difficult to determine how common the fission-fusion type of social organization is within the class Mammalia, since information on the compositional stability of groups is so often lacking. Thus, in some subdisciplines (e.g. primatology) fission-fusion societies are considered to be rare and that groups by definition have stable membership, where any changes in composition occur at a slow rate, as the result of demographic processes of birth, death, immigration, and emigration (Richard 1985). However, a number of natural history descriptions of particular mammal species provide evidence suggesting that many phylogenetically distant mammals possess this type of social organization (Table 1).

The objective of this paper is to attempt to identify the selective advantages maintaining fission-fusion social organizations in a variety of mammal species. Two ecologically based explanations for the evolution of fission-fusion social organizations are proposed and mammal species for which each of the explanations might apply are tentatively identified. To meet this objective I have primarily relied on published studies, although I also draw upon information from the previous chapters which discuss the foraging strategies and social organizations of the spider and howling monkeys of Santa Rosa National Park, Costa Rica.

I propose that there are two similar processes operating to maintain fission-fusion social organizations in mammals. Both processes deal with foraging efficiency and changing resource states, but the first process deals with foraging efficiency as related to travel cost and patch depletion, while the second process deals with foraging efficiency as related to the success of capturing prey. I suggest that when resources are such that they permit many social animals to efficiently forage together, animals will be found in large groups. In contrast, when resources are such that only a few social animals can efficiently forage together, they will be found in small groups. If foraging efficiency is related to group size and if resource conditions change over short periods of time, I propose that fission-fusion social organizations can evolve. This approach assumes that there exists advantages to group living in the social mammals discussed.

1) Fission-Fusion Societies as Related to Patch Depletion and Travel Costs

Patches Depleted on the Short Term

The abundance and distribution of resources can influence an animal's foraging efficiency by affecting its travel costs. Animals must forage over an area that adequately meets their energetic and nutritional needs. If animals deplete the resources in an area by their use, an increase in group size will increase the distance that must be travelled to find adequate food supplies (food abundance remaining constant). Thus, individuals in a large group that foraged in an area large enough to meet the needs of all group members, would spend more energy on travel than would be the case if they had fed in smaller groups or alone (Milton and May 1976). With an increase in the time spent travelling, some point will be reached at which the energy spent in travel exceeds that obtained by feeding, and a smaller group will be advantageous. In this fashion, ecological factors can influence foraging efficiency and thereby constrain a group to a particular size.

When the abundance and/or distribution of resources change and there are advantages to living in a group (Alexander 1974), a fission-fusion type of social organization will allow animals to use available food resources most efficiently, while still acquiring the advantages of group living. I propose that the repeated splitting and joining of subgroups observed in many

fission-fusion societies is a response to changes in the abundance and distribution of their food resources and an attempt to forage efficiently.

A number of studies provide descriptive evidence supporting this line of reasoning. Leuthold (1974) described the lesser kudu (Tragelaphus imberis) of Tsavo National Park, Kenya as living in groups of variable composition, and stated that small groups may temporarily join to form larger units. The lesser kudu is a medium sized antelope that lives in areas of grassland with scattered patches of bush. The seasonal movement patterns of these animals correspond closely to the time of leaf loss of many of the deciduous trees. Leuthold suggested that in seasonal habitats such as this, with scarce or erratic food supplies, flexiblity in social organization is advantageous.

Similarly, Sinclair (1974,1977) demonstrated that the size of a herd of African buffalo (Syncerus caffer) was flexible and was related to both habitat type and season. Pienaar (1969) suggested that a positive relationship existed between herd size and the distance that must be travelled to find fresh grazing areas. Sinclair (1974) extended this argument by stating that the "local patches of suitable habitat are not large enough in any event to accommodate the very big herds" and subsequently that the "splitting of herds was related to the fragmentation of preferred habitats".

Rubenstein (1986) described the social organizations of horses and zebras. At one study site, no permanent associations occurred between male and female horses. At this site, females leave and enter groups depending on the food resources found in the area. Rubenstein described that "When food patches are relatively large groups grow as smaller groups fuse. But as soon as aggregations move to smaller patches, fissioning occurs.

In giraffes, for which no permanent associations have been found to occur (Foster and Dagg 1972, Leuthold 1977, Leuthold and Leuthold 1972), the distance groups travel changes with season (Leuthold and Leuthold 1972). Seasonal changes in food abundance and distribution have been documented in a number of African ungulates (Leuthold 1977, Leuthold and Leuthold 1975). As predicted by the ecological argument proposed, for giraffes these changes in food resources corresponded to a seasonal change in group size (Foster and

Dagg 1972).

In chapters 3 and 5, I demonstrated that the spider monkeys of Santa Rosa National Park, Costa Rica likely deplete the food patches they use and that this results in individuals in large subgroups having to travel more than individuals in small subgroups. In addition, it was possible to predict the relative size of the spider monkey subgroups from the size, density, and distribution of food trees. It was further demonstrated that the resources available to the spider monkeys changed over short periods of time. Thus, I suggested that the fission-fusion social organization of the spider monkey is adapted to obtain the advantages from living in a group, while still efficiently using resources that can change over a short period.

The argument outlined to explain the maintenance of fission-fusion social organizations is based on a number of assumptions. For any animal species, if the assumptions are not met, the proposed argument cannot be a valid explanation of their social organization. Thus, it is valuable to examine how broadly the assumptions of the argument are met by those species in which group size varies frequently over a short period of time. First, it was assumed that the animals are capable of responding to changes in the availability of resources by either changing their movement patterns and/or by changing group size. Studies of a number of mammalian species have shown that as group size increases, the area that is searched increases. Pienaar (1969) found that large herds of African buffalo travelled longer distances than smaller herds. Anderson (1981), in studying a group of chacma baboons (Papio ursinus) with a fission-fusion type of social organization, found that the size of a group was significantly related to day range length. She further demonstrated that day range length varied in correspondence with food availability. Similarly, van Schaik et al. (1983) showed that the distance long-tailed macaques (Macaca fascicularis) travelled in a day increased with group size. Ruiter (1986) observed two groups of Cebus olivaceus and documented that the smaller group travelled less than the larger group.

Other studies have shown that animals respond to the changes in the availability of their food resources by changing group size. Leuthold (1976, 1977) stated that the mean size of elephant groups changed in relation to environmental conditions. Kitchen (1974) discovered

that the size of pronghorn sheep groups changed frequently and was positively related to the mean weight of forage in an area. Lynch (1974) demonstrated that a captive group of Merino sheep tended to fragment when food resources became scarce. Lagory (1986) comparing groups of white-tailed deer (Odocoileus virginiatus) in different types of habitats, observed that group size varied directly with food abundance. Wrangham (1986) reported that chimpanzee subgroups were smallest when their food resources occurred at a low density, and that the largest subgroups were seen at large food trees.

A second assumption of the argument proposed to explain the adaptive value of fission-fusion social organization is that the resources used by these animals occur in patches and that animals must move between food patches. Largely as a result of the difficulty in choosing the appropriate spatial and temporal scale, this assumption is difficult to test quantitatively. Kitchen (1974) examined the weight of forage per unit area in sites used by pronghorns and found that the weight of food varied widely between areas and the animals selected areas with greater amounnts of food.

Quantitative examination of the distribution of food resources are rare in mammals with fission-fusion types of social organization; however, many studies provide qualitative assessments. Schaller and Minza (1974) reported that a herd of Punjab Urial (Ovis orientalis) was unstable in composition, with the only lasting association being between the ewe and her young, and stated that food resources were sparse and scattered. Leuthold (1970) described female herds of impala (Aepyceros melampus) as being unstable in composition and number and described their food as being distributed in clumps. Bradbury (1977,1981), and Bradbury and Vehrencamp (1976) described considerable movement of female Saccopteryx bilineata (an insectivorous bat) between harems, and suggested that the compositional stability of the harems was low. Further, they described the food resources of this species as being "patchy".

A third assumption of the argument proposed to explain the evolution of fission-fusion societies is that foraging efficiency will decrease as group size increases (when food abundance is constant). For a number of primate species high levels of aggression and interference occur when large groups use small patches. Aggression at feeding sites will likely

decrease foraging efficiency. Klein (1972) and Klein and Klein (1977) found that aggression increased when spider monkeys (Ateles bezebuth) fed in small trees, and Chivers (1977) observed the same relationship with siamangs (Symphalangus syndactylus). Waser (1977) observed that aggression by mangabeys (Cercocebus albigena) increased in small trees when the number of individuals feeding increased. Sussman and Richard (1974) found that lemurs were aggressive when food was limited to small areas. Van Schaik et al. (1983) found a monotonic increase in the level of social tension when the size of long-tailed macaque (Macaca fascicularis) groups increased. Ruiter (1986) in a study of two groups of Cebus olivaceus using the same area of forest, found that the larger group had higher levels of agonism than the smaller group. Janson (1985a,b) in a study of Cebus apella, demonstrated that when the abundance of fruits and insects were low, competition between group members was intense and that dominant animals had significantly greater energy intake than did subordinates. Kaufmann (1974) suggested that the frequent encounters of male whiptail wallabies at restricted feeding sites was both stressful and wasteful of time and energy (cf Stacey 1986). All of these examples suggest that as group size increases, aggression will increase, and that under these conditions the efficiency of obtaining a limited food resource will likely decrease.

Patches Not Depleted or Depleted Over The Long Term

Fission-fusion societies can form when resources are not depleting in the short term, but deplete seasonally. This situation frequently occurs in ungulates where large herds form in the rainy season and feed on the slowly depleting productive grasses. In the dry season these large herds fragment as food abundance declines and are often described as taking advantage of localized resources, such as the fresh grasses sprouting in burnt areas. Typical examples of this pattern include the uganda kob (Leuthold 1966), African buffalo (Jarman 1974, Sinclair 1977), defassa waterbuck (Hanks et al. 1969, but see Spinage 1969), gazelles (Estes 1977) and whiptail wallabies (Kaufmann 1974).

There are a number of excellent documentations of animals responding to non-depleting resources by changing their social organization. MacDonald (1979) described a

flexible pattern of social organization in different groups on golden jackals (Canis aureus). When jackals had access to large non-depleting clumped resources (provisioning sites and dumps), they permanently banded together into cohesive social groups of between 10 and 20 members. However, in the more typical situation, jackals have access to depleting resources that are more uniformly distributed. Under these conditions jackals occur as pairs (Schaller 1967, Van Lawick and Van Lawick-Goodall 1970). The only difference between the example just described for jackals and that outlined for a variety of bovids, is that the resources used by the jackals in MacDonald's (1979) study were permanently abundant and clumped, whereas the abundance of the food available to the bovids changes on a seasonal basis. Similarly, Dunnett (1962), and Holsworth (1967) observed that the normally solitary quokkas (Setonix brachyurus) aggregate at waterholes and garbage dumps.

The ecological conditions which favour the aggregation of groups differs between when resources are depleted over a long period and when they are depleted rapidly. When food resources are depleted over a long period of time, large aggregations form when food resources are clumped, as a result of animals coming together at the locations containing food. In contrast, when patches are depleted on the short term, small aggregations occur when resources are clumped. This results because large groups deplete patches rapidly; thus animals must visit more patches, and it becomes inefficient to do so because of the cost of travel.

2) Fission-Fusion Social Organizations As Related to Capture Efficiency

A number of authors have suggested that for carnivores the efficiency of obtaining different types of prey is a function of group size, and have documented that as the abundance of the different types of prey changes (usually on a seasonal basis), the size of the observed groups change. This situation has been most thoroughly documented in the case of foraging lions (Schaller 1972, Caraco and Wolf 1975, Clark 1986). In the dry season large prey are scarce for the lions of Serengeti National Park, Kenya, and they feed primarily on Thomson's gazelles (Gazella thomsoni). The capture of these small gazelles, is most efficiently done for lions hunting in pairs. With the return of the rains, the abundance of large ungulates, such as wildebeest, increases. When hunting these large animals, a larger

group increases the efficiency of capture. Corresponding to the change in availability of these different types of prey, and thus the hunting efficiency of groups of different sizes, the size of the observed subgroups changed (Schaller 1972, Caraco and Wolf 1975).

A similar argument may explain the change in group size of the Atlantic bottlenose dolphin (Tursiops truncatus). In the winter months this dolphin feeds primarily on large schools of anchovies (Wursig 1978, 1979, Wursig and Wursig 1977, 1979a,b). The efficiency of hunting anchovies appears to increase with group size. Not only does the probability of locating a school increase with group size, but large groups may also allow the dolphins to make a more efficient "surround net", which serves to keep the fish in the area where dolphins can feed (this "surround net" was described by Wursig and Wursig 1979 for the dusky dolphin, Lagenorhynchus obscura, and I assume that it may also operate for the bottlenose dolphin). In the summer, the anchovie schools are not available and the dolphins tend to feed on large solitary fish. When hunting these fish, little if any aid is received from conspecifics in locating or capturing prey. The change in the types of prey that are available, and thus in the size of the groups which were most efficient for capturing prey, corresponded to a change in the size of the observed groups from a mean of 14 individuals in the summer, to a mean of 20 in the winter (Wursig 1979). A similar explanation may account for the seasonal changes in group size seen in other cetaceans that appear to have a fission-fusion type of social organization (Wursig 1986, Johnson and Norris 1986; dusky dolphins, bottlenose dolphins, Wursig and Wursig 1979, Wursig 1979b; bottlenose and humpback dolphins, Saayman and Talyer 1973; sinner dolphin, Norris and Dohl 1980; minke whales, Gaskin 1982; harbor porpoises, Gaskin 1982). Kruuk (1966, 1972) presents a similar example for the foraging groups of hyaenas (Crocuta crocuta).

One special case of a fission-fusion society that deserves mentioning, deals with animals that must regularly return to a refuge (Hamilton and Watts 1970). Examples among social mammals include the hamadryas baboon (Papio hamadryas; Kummer 1968) and the fur seal (Callorhinus ursinus; Bartholomew and Hoel 1953). Probably because of the scarcity of

safe sleeping sites, hamadryas baboons congregate at night in troops of as many as 150 individuals, which may, depending on the environmental conditions, split into one-male groups during the day when they are foraging (Kummer 1968). A similar situation can occur with savanna baboons (Papio cynocephalus) when they congregate at sleeping trees (Altmann and Altmann 1970, Hamilton 1982).

Possible Benefits of Fission-Fusion Social Organizations

Many of the species that have been identified as exhibiting fission-fusion social organizations actively defend territorial boundaries. To be able to reliably defend a boundary, the animals must encounter the edge of their territory frequently enough to establish ownership and detect intruders (Mitani and Rodman 1979). The frequency with which a group encounters its territorial boundaries is a function of the rate that the groups moves and the size of the territory. Mitani and Rodman (1971) demonstrated that primates with short day ranges that require a large home range will be unable to encounter their territorial boundary frequently, and thus tend to be non-territorial. However, chimpanzees and spider monkeys appear to be exceptions to this generality. A species which requires a large home range, but has a day range that is not long enough to allow adequate defense of their boundaries, may increase the rate at which group members encounter their territorial boundaries by adopting a fission-fusion social organization. By dividing into subgroups, individuals can maintain short day ranges while the group as a whole increases its rate of encounter with its territorial boundaries. For that process to assist in maintaining the integretiy of a territory, the outcome of territorial encounters must not depend on the relative sizes of the contesting parties. However, a number of studies have shown that a small number of territorial owners can often displace much larger groups of intruders (Richard 1985).

Mitani and Rodman (1979) calculated an index of defendability as:

$$D = \frac{d}{(4A/\ )}$$

where d is the average day range and A is the group's home range size. These authors suggest that all primate groups that are territorial have an index of 1.0 of greater, and that

non-territorial primate species have an index greater than 1. Using this calculation, Mitani and Rodman grouped the chimpanzee with species unable to defend a territory. Yet, Wrangham (1977) described the relationships between communities as aggressive and Nishida (1983) described the chimpanzees of Mahale as having "well defined and traditional boundaries". If instead of considering the chimpanzee groups to move as a single cohesive unit, as Mitani and Rodman did, they are considered to move as independent subgroups, the northern community studied by Wrangham (1977) and Wrangham and Smuts (1980) would consist of 19 subgroups (median group size used) each travelling an average of 3.9 km/day. Under those conditions chimpanzees should be capable of defending a territory (D=18.6), the index more appropriately represents the observed conditions, and chimpanzees are no longer an unexplained exception.

In addition to being beneficial for territorial defence, adopting a fission-fusion social organiation may allow a group's home range to be sampled more intensively for the arrival of new food sources. If information regarding the location of new feeding sites can be transmitted between individuals (see Menzel 1971, 1973, Ward and Zahavi 1973), this additional sampling can benefit all group members, many of which may be related. Information transfer may occur when subgroups fuse, or at central sleeping sites that animals use on a regular basis, such as is found in spider monkeys, hamadryas baboons, and whiptail wallabies (in this case the process may be similar to the "Information Center Hypothesis" proposed by Ward and Zahavi 1973 for communially roosting birds).

Conclusion

This review suggests that the fission-fusion type of social organization may be relatively common in mammals and that this type of social organization can arise from two basic processes. In the first case, as the density and distribution of resources change, animals alter their group size in an attempt to forage efficiently. If patches are depleted rapidly animals compensate for increased travel costs associated with large groups, by fragmenting. If patches are depleted very slowly or seasonally, animals congregate in areas of high food density. In the second situation the efficiency of prey capture changes with group size and the

types of prey available changes. The two processes are in many ways similar. In both situations, changes in group size represent the attempts made by individuals to maintain adequate foraging efficiency as the environmental conditions change. The first process deals with foraging efficiency as related to travel costs and patch depletion, and the second process deals with foraging efficiency as related to capture success. In addition to such ecological pressures favouring fission-fusion societies, animals with this type of social organization may be better able to defend their territorial boundaries and sample the environment, than animals that have cohesive closed groups.

In conducting this survey it became evident that although a number of mammals appear to associate in a pattern that suggests they possess a fission-fusion type of social organization, there are many differences in the form that this social organization can take. For example, why do some species have strong dominanace heirarchies whereas others do not; why in some species do males emigrate between groups while in others females or even both sexes leave their natal group; why in some species do the males form tight social bonds, while in others they do not; and why does the integrity or relative level of closure at the community level differ between species. Addressing questions such as these may help develop generalizations as to what forces shape social organizations. In unraveling the answers to such questions it seems likely that investigators must first address factors influencing female behavioural patterns, for a number of authors have suggested that male behaviour is adapted to the behaviour of females (Wrangham and Rubenstein 1986). In addition, it seems necessary to not only examine factors such as predation and resource states, but also social variables should be considered, since social factors may themselves be important in structuring of social groups.

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Table 1.
A tentative list of some of the species of mammals thought to possess a fission-fusion type of social organization.

Taxon	Species	Common Name	Source
Marsupialia			
	Macropus parryi	whiptail wallaby	Kaufmann 1974
	Macropus giganteus	grey kangaroos	darman and Southwood 1986, Kaufmann 1975
Artiodactyla			
	Bison bison	bison	Lott and Minto 1983
	Giraffe sp.	giraffe	Foster and Dagg 1972, Leuthold 1977
	Capra sp.	feral goats	Riney and Caughley 1959
	Hippotragus niger	sable	Estes 1974
	Kobus kob	Uganda kob	Leuthold 1966,1977
	Kobus defassa	waterbuck	Kiley-Worthington 1965, Hanks et al. 1969
	Aepyceros sp.	impala	Jarman 1974,Leuthold 1970,1977, Jarman and Jarman 1973
	Tragelaphus imberis	lesser kuda	Leuthold 1971,1977
	Redunca sp.	reedbuck	Leuthold 1977
	Syncerus caffer	African buffalo	Sinclair 1971,1977, Pienaar 1969 Gosling 1986
	Ovis orientalis	urial	Schaller and Minza 1974
	Equus sp.	horse	Rubenstein 1986, Klingel 1974
Carnivora			
	Crocuta crocuta	hyaena	Kruuk 1966,1972, Frank 1986a,b
	Panthera leo	lions	Schaller 1972, Caraco and Wolf 1975
Cetacea			
	Lagenorhynchus sp.	dusky dolphin	Wursig and Wursig 1979,
	Tursiops truncatus	bottlenose dolphin	Wursig 1977,1979
	Sousa plumbea	humpbacked dolphin	Saayman and Talyer 1973
	Stenella sp.	spinner dolphin	Norris and Dohl 1980
Chiroptera			
	Saccopteryx bilineata		Bradbury 1977,1981, Bradbury and Vehrencamp 1976
Primates			
	Ateles sp.	spider monkeys	Klein 1977, Klein and Klein 1977, Fedigan and Baxter 1984
	Cercopithecus aethiops	vervet	Chapman unpublished data
	Macaca fascicularis	long-tailed macaque	Van Sdaik et al. 1983
	Papio ursinus	chacma baboon	Anderson 1981
	Papio hamadryas	hamadryas baboon	Kummer 1968
	Pan troglodytes	chimpanzee	Wrangham 1977,1980,1986
Proboscidea			
	Loxodonta africana	Africa elephant	Kurt 1971, Laws 1971, Leuthold 1976,1977
Sirenia			
	Trichechus manatus	Manatee	Reynolds 1979

VITA

Colin A. Chapman

December 1986

Colin Austin Chapman

Date of Birth - May 20, 1959

Place of Birth - Edmonton, Alberta, Canada

Marital Status - Married

Citizenship - Canadian

Present Home Address :

#307 10159-118 st.

Edmonton, Alberta

Canada, T5K 2K1

Phone Number - (403)-488-3394

University Address:

Biology Department

McGill University

1205 Dr. Penfield Ave.

Montreal, Quebec

Canada, H3A 1B1

Phone Number - (514)-392-5888

Degrees Held :

Ph.D. in Anthropology and Zoology

Received at the University of Alberta in 1987

Area of Specialization : Primate Behavioural Ecology

Thesis Title : Foraging Strategies, Patch Use, and Constraints on Group Size in Three Species of Costa Rican Primates.

Supervisors : Drs. L.M. Fedigan and J. Murie

Masters in Anthropology

Received at the University of Alberta in 1983

Area of Specialization : Primate Behavioural Ecology

Thesis Title : Behavioural Ecology of the St. Kitts Vervet

Supervisor : Dr. Linda M. Fedigan

B.Sc. (Honours) in Zoology received at the University of Alberta in 1981

Research and Teaching Interests:

Primate Behavioural Ecology

Evolution of Primate Social Systems and Group Size

Statistical Data Analysis

Biogeographical Theory

Primate Demography

Plant Phenology and Distributions

Plant Animal Interactions (Seed Dispersal)

Transect Methodology

Vocalizations and Communication

Memberships of Professional Societies

Animal Behaviour Society

Association for Tropical Biology

Awards Received:

University of Alberta Dissertation Fellowship - Received September 1986

Province of Alberta Graduate Fellowship - Received September 1985

University of Alberta Graduate Intersessional Bursary - Received May 1985

Natural Sciences and Engineering Research Council of Canada Postgraduate

Scholarship - Received

1984 - 1985, 1983 - 1984, and 1982 - 1983

University of Alberta Graduate Bursary

Received 1981

University of Alberta Graduate Assistantship

Received 1981

Natural Sciences and Engineering Research Council of Canada Summer Undergraduate Research Awards - Received

1979 and 1980

Province of Alberta Scholarship

Received four times from 1977 to 1981.

Woodwards Scholarship

Received four times from 1977 to 1981.

Publications:

(1) Selection of Secondary Growth Areas by Vervet Monkeys (Cercopithecus aethiops).

C.A. Chapman 1987 (In Press).

American Journal of Primatology

(2)Social Responses to the Traumatic Injury of a Juvenile Spider. Monkey

C.A. Chapman and L.J. Chapman 1987.

Primates 28(2):?

(3) Development of Howling Monkey Twins (Alouatta palliata) in Santa Rosa National Park, Costa Rica.

C.A. Chapman and L.J. Chapman 1986.

Primates 27:377-381.

(4) A Census of Alouatta palliata and Cebus capucinus in Santa Rosa National Park, Costa Rica.

L.M. Fedigan, L. Fedigan, and C.A. Chapman 1986.

Brenesia 23:309-322.

(5) Boa constrictor Predation and Group Response in White-Faced Cebus Monkeys.

C.A. Chapman 1986.

Biotropica 18:171-172.

(6) Distribution of Tropical Rain Forest Primates.

C.A. Chapman 1986.

In : D.M. Taub and F.A. King (eds.),

Current Perspectives in Primate Social Dynamics. pp.194-205.

Van Nostrand Reinhold Co., New York.

(7) The Influence of Habitat on Behaviour in a Group of St. Kitts Green Monkeys.

Colin Chapman 1985.

Journal of Zoology 206:311-320.

(8) A Demographic Model of Colonization by a Population of St. Kitts Vervets.

L.M. Fedigan, L. Fedigan, C.A. Chapman, and M.T. McGuire 1985.

Folia Primatologica 42:194-202.

(9) Territoriality in the St. Kitts Vervet (Cercopithecus aethiops).

C.A. Chapman and L.M. Fedigan 1984.

Journal of Human Evolution 13:677-686.

(10) Direct Observation of Habitat Use by Northern Pike.

C.A. Chapman and W.C. Mackay 1984.

Copeia 1984:255-258.

(11) Versatility of Habitat Use by a Top Aquatic Predator.

C.A. Chapman and W.C. Mackay 1984.

Journal of Fish Biology 25:109-116.

(12) Speciation of Tropical Rain Forest Primates of Africa : Insular Biogeography.

C.A. Chapman 1984.

African Journal of Ecology 21:297-308.

In Preparation

(13) Patch Use and Patch Depletion by the Spider and Howling Monkeys of Santa Rosa National Park, Costa Rica.

C.A. Chapman (Submitted).

(14) A Comparison of Transect Methods of Estimating Population Density of Costa Rican Primates

C.A. Chapman, L.M. Fedigan, and L. Fedigan (Submitted).

(15) Capture and Marking Monkeys in Santa Rosa National Park, Costa Rica.

K. Glander, L.M. Fedigan, L. Fedigan, and C.A. Chapman (Submitted).

(16) Primate Seed Dispersal: The Fate of Dispersed Seeds.

C.A. Chapman (Submitted).

(17) Age and Sex Differences in Foraging Strategies and Behaviour in the St. Kitts Vervet Monkey.

C.A. Chapman

(18) Ecological and Demographic Influences on the Pattern of Association in a Group of St. Kitts Vervets.

C.A. Chapman, L. Fedigan, and L.M. Fedigan

(19) Ecological Constraints on Group Size in Three Species of Neotropical Primates.

C.A. Chapman

(20) Flexibility in Diets of Three Species of Costa Rican Primates.

C.A. Chapman

(21) Patterns of Foraging and Range Use by Three Species of Neotropical Primates.

C.A. Chapman

(22) Food Availability: The Responses of a Tropical Frugivore.

C.A. Chapman and L.J. Chapman

(23) Social Structure of the Spider Monkey : Is It Like That of the Chimpanzee?

C.A. Chapman and L.M. Fedigan.

(24) Post-Weaning Resource Competition and Sex Ratios in Spider Monkeys.

C.A. Chapman, L.M. Fedigan, L. Fedigan, and L.J. Chapman.

(25) Reproductive Strategies of Primates : The Influence of Body Size and Diet on Litter Size.

C.A. Chapman, S. Walker, and L. Lefebrve

(26) Origins of Fission-Fusion Societies in Mammals.

C.A. Chapman

(27) Use of Visual Census Techniques for Estimating Density and Population Size in Schooling and Solitary Fish

L.J. Chapman and C.A. Chapman

Published Abstracts of Papers Given

(1) Ecological Constraints on Group Size for Three Species of Neotropical Primates.

American Journal of Primatology 10:394.

(2) Seasonal Shifts in Resource Use and the Interspecific Interactions of Three Species of Neotropical Primates.

Canadian Journal of Anthropology 4(suppl.):50-51.

(3) Behavioural Ecology of the St. Kitts Vervet.

Canadian Journal of Anthropology 4(suppl.):30.

(4) Speciation of High Forest Primates of Africa : Insular Biogeography

International Journal of Primatology 3:270.

Papers Delivered

(1) Patch Use By Primates

Poster Presented at the Behavioural Ecology Meetings

Albany, New York, October 1986

(2) Ecological Constraints on Group Size for Three Species of

Neotropical Primates.

Presented at American Society of Primatologists

Austin, Texas, June 1986.

(3) Foraging Strategies and Group Size in Three Species of Neotropical Primates.

Presented at SQBEC, Quebec City, November 1985.

(4) Seasonal Shifts in Resources Use and the Interspecific Interactions of

Three Species of Neotropical Primates.

Presented at the Canadian Association for Physical Anthropology.

Edmonton, Alberta, October 1984.

(5) Behavioural Ecology of the St. Kitts Vervet.

Presented at the Canadian Association for Physical Anthropology.

Montreal, Quebec, October 1983.

(6) Speciation of High Forest Primates of Africa : Insular Biogeography

Presented at the IXth International Society of Primatologists.

Altanta, Georgia, August 1982

Related Experience

Field Work:

February 1986 to August 1986, January 1985 to July 1985, and

January 1984 to August 1984 :

Research on the Foraging Strategies of Alouatta palliata, Cebus capucinus

and Ateles geoffroyi in Santa Rosa National Park, Costa Rica.

Thesis research supervised by Dr. Linda Fedigan and Dr. Jan Murie

May 1985 and February 1986 :

Darting, chemical immobilizing, and radio tracking primates in Santa Rosa National Park.

Research in conjunction with Dr. Ken Glander and Dr. L.M. Fedigan.

June 1983 to September 1983:

Census of Alouatta palliata and Cebus capucinus in Santa Rosa National Park, Costa Rica.

April 1982 to December 1982:

Research on the primate behavioural ecology of the St. Kitts Vervet.

Thesis research supervised by Dr. Linda Fedigan.

May 1981 to September 1981:

Research involving a survey of the tropical rain forest primates of Central America and the Caribbean.

Research supervised by Dr. L.M. Fedigan.

May 1980 to September 1980:

Research dealing with the habitat utilization of northern pike (Esox lucius) in a Boreal Lake in Northern Alberta.

Research Supervised by Dr. W.C. McKay.

Research Assistance:

August to September 1984:

Computer analysis for Alberta Fish and Wildlife.

September to December 1983:

Research Assistant for Dr. Linda M. Fedigan involving computer analysis of demographic data.

December to May 1983:

Research assistant for Dr. Linda Fedigan involving computer analysis of primate behavioural data

December to April 1982:

Research assistant for Dr. C. Schweger, involving the study of quaternary environments.

May 1979 to September 1979:

Research assistant for Dr. D. Boag studying the population ecology of the spruce grouse.

May 1978 to September 1978:

Technician II for the Province of Alberta involved in an ecological survey of the Kananascas Park area.

May to September 1977 and 1976:

Program specialist for the Edmonton City Zoo. This position involved feeding and care of zoo animals.

Teaching Experience:

Teaching assistant involving teaching a laboratory for a course titled "Man and His Environment", a conservation oriented course offered by the Zoology Department of the University of Alberta.

I taught this lab for a number of years in succession starting in 1979 until 1983.

September to December 1982:

Teaching assistant in Anthropology

Invited Lectures

McGill University, Biology Department - December 1986

University of Montreal, Anthropology Department - December 1986

McGill University, Biology Department - October 1985

Organization of Tropical Studies - June 1985